Wooded or treeless pastures?
Linking policy, farmers' decisions and biodiversity

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Abstract
Worldwide, biodiversity conservation is one of the key challenges for a sustainable future of nature and society. It is particularly important to preserve high quality habitats within otherwise intensively managed agricultural landscapes. Within the European Union (EU), farmers are highly dependent on agricultural subsidies through the Common Agricultural Policy (CAP), which hence have a strong influence on management and biodiversity. In European agricultural landscapes, wooded pastures form important habitats that contribute to landscape level heterogeneity and high local biodiversity, values which are often closely linked to trees. Unfortunately, many of these values were put at risk when a tree density limitation was introduced within the CAP, encouraging farmers to keep pastures open and ensuring grazing management. However, limiting tree density to a specific number to increase biodiversity finds little basis in the scientific literature. The main objective of this thesis is therefore to investigate how different measures of biodiversity across multiple taxa are affected by tree density and to study the farmers' perspective on this CAP regulation. Wooded pastures in the biosphere reserve Östra Vätterbranten in southern Sweden were used as study sites. This thesis shows that encouraging farmers to cut trees to receive subsidies weakens the link between social and ecological values of wooded pastures, with potential subsequent losses in biodiversity. Trees were almost exclusively positive for biodiversity within this study system, increasing the species richness of plants, birds and bats. However, functional diversity across these taxa were mainly affected by other vegetation attributes within and around the pastures, such as shrub density and surrounding forest cover. A seed sowing experiment showed how trees partly shape plant communities already at the germination stage. Further, responses of functional diversity was mainly driven by resource use related traits among plants and birds, whereas bat functional diversity responses were mainly determined by their ability to manoeuvre through the micro-habitats of wooded pastures. Based on this thesis, I conclude that the tree density limit proposed by the EU has failed to capture the unique biological values of continuously managed wooded pastures and that the social-ecological links between policy, management and biodiversity are threatened by number specific governance of nature. It is therefore promising that the EU in November 2017 announced to open up for excluding the tree density focus in the CAP. Further development of the CAP can benefit from the findings of this thesis, revealing important knowledge gaps on biodiversity patterns in relation to trees in pastures.

Keywords: bat, biodiversity, bird, canopy cover, Common Agricultural Policy, European Union, farmer, functional diversity, germination, grassland, multi-taxon, pasture, plant, policy, seed sowing, tree density, trees.

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`I thought that trees were good for the environment?'

- Anonymous farmer
Abstract

Worldwide, biodiversity conservation is one of the key challenges for a sustainable future of nature and society. It is particularly important to preserve high quality habitats within otherwise intensively managed agricultural landscapes. Within the European Union (EU), farmers are highly dependent on agricultural subsidies through the Common Agricultural Policy (CAP), which hence have a strong influence on management and biodiversity. In European agricultural landscapes, wooded pastures form important habitats that contribute to landscape level heterogeneity and high local biodiversity, values which are often closely linked to trees. Unfortunately, many of these values were put at risk when a tree density limitation was introduced within the CAP, encouraging farmers to keep pastures open and ensuring grazing management. However, limiting tree density to a specific number to increase biodiversity finds little basis in the scientific literature. The main objective of this thesis is therefore to investigate how different measures of biodiversity across multiple taxa are affected by tree density and to study the farmers’ perspective on this CAP regulation. Wooded pastures in the biosphere reserve Östra Vätterbranterna in southern Sweden were used as study sites. This thesis shows that encouraging farmers to cut trees to receive subsidies weakens the link between social and ecological values of wooded pastures, with potential subsequent losses in biodiversity. Trees were almost exclusively positive for biodiversity within this study system, increasing the species richness of plants, birds and bats. However, functional diversity across these taxa were mainly affected by other vegetation attributes within and around the pastures, such as shrub density and surrounding forest cover. A seed sowing experiment showed how trees partly shape plant communities already at the germination stage. Further, responses of functional diversity was mainly driven by resource use related traits among plants and birds, whereas bat functional diversity responses were mainly determined by their ability to manoeuvre through the micro-habitats of wooded pastures. Based on this thesis, I conclude that the tree density limit proposed by the EU has failed to capture the unique biological values of continuously managed wooded pastures and that the social-ecological links between policy, management and biodiversity are threatened by number specific governance of nature. It is therefore promising that the EU in November 2017 announced to open up for excluding the tree density focus in the CAP. Further development of the CAP can benefit from the findings of this thesis, revealing important knowledge gaps on biodiversity patterns in relation to trees in pastures.
Sammanfattning

Hög biologisk mångfald är av yttersta vikt för en hållbar framtid, både för naturen och för människan. Varterefler vi människor blir fler och fler ökar också behovet av att producera mer mat, vilket innebär att mer och mer mark tas i anspråk för jordbruk. Inom Europa är dock många höga biologiska värden knutna till just jordbruksmark, men då till de låg-intensivt brukade markerna så som naturbetesmarker och slätterängar. Detta tyder på att med rätt skötselmetoder inom jordbrukslandskapet finns det stor potential att bevara mycket av den biologiska mångfalden, men troligen krävs det starka ekonomiska drivkrafter för att uppnå detta.

Inom jordbrukssektorn utgör ersättningar från EU och nationella myndigheter en stor del av brukares ekonomi, och har på så sätt stor effekt på skötsel av jordbruksmark. I jordbrukslandskapet återfinns fortfarande en liten andel så kallade trädbärande betesmarker. Dessa har höga biologiska värden, både som habitat för många organismer men också genom att bidra till variation i landskapet. I Sverige har dessa marker traditionellt sett bestått av varierande täthet av träd, i många fall så täta att de idag klassas som skog. Som ett slag mot dessa värdefulla miljöer introducerade EU år 2003 en regel kring hur många träd brukare får ha på sina marker för att få så kallat gårdsstöd, med målet att uppmuntra fortsatt brukande och upprätthållande av öppna marker i jordbrukslandskapet.

Denna gräns sattes till 50 träd per hektar, ändrades senare till 100 träd per hektar, och nyligen annonserade EU att denna begränsning skulle tas bort ur regelverket. Trots en till synes lättfanterlig gräns (att räkna antal träd) medförde denna gräns stora svårigheter rent byråkratiskt och resulterade i både övergivning av marker och nedhuggning av träd, liksom konflikter mellan brukare, myndigheter och naturvårdsintressen. En intressant aspekt av denna trädregel är hur godtyckligt den sattes till 50 träd per hektar. Det finns väldigt lite vetenskaplig grund för en sådan gräns, och när man tittar närmare på problemet uppdagas en relativt stor kunskapslucka gällande hur biologisk mångfald påverkas av just träd i naturbetesmarker. Denna avhandling undersöker därför hur trädregeln påverkat brukare och hur träd faktiskt påverkar biologisk mångfald. Biosfärområdet Östra Vätterbranterna i södra Sverige har använts som studieområde, där mångfalden av växter, fåglar och fladdermöss undersökt parallellt med en intervjustudie med brukare i området.

Denna avhandling består av en sammanfattande syntes av fyra separata studier i form av artiklar/manuskript. Den första fokuserar på brukares syn på trädregeln (och andra ekonomiska styrmedel) och skötseln av naturbetesmarker. I nästföljande studie undersöks hur mångfald och artssammansättning av växter påverkas av träd och andra faktorer i 64 betesmarker. För att få en bättre förståelse av dessa resultat genomfördes i den tredje studien ett frösåningsexperiment inom fyra av dessa betesmarker för att undersöka hur olika trädarter påverkar olika växtarters groning. I den sista studien undersöks artrikedom och funktionell mångfald av växter, fåglar och fladdermöss i relation till träd och andra vegetationsstrukturer i 21 betesmarker. Funktionell mångfald är ett mått på hur stor variation det finns bland egenskaper hos arterna, i det här fallet inom en betesmark, vilket påverkar hur arterna använder sig av och påverkas av sin omgivande miljö.

De intervjuade brukarna såg varken enbart negativt eller positivt på den trädregel som nu gällt i ungefär ett decennium, även om tendenser till viss frustration kunde märkas. Framförallt ledde denna regel till en rad konflikter mellan brukare och myndigheter, som dock förbättrats på senare år. Däremot ansågs skötseln av träd sedan länge vara en del av arbetet med betesmarker, där trädens kulturella, ekologiska och estetiska värden framhölls som viktiga argument för att bevara dem. Dessutom uppmärksammade många brukare hur vanliga trädarter togs bort till fördel för andra mer unika arter, vilket i sin tur givetvis påverkar den biologiska mångfalden, i de flesta fall positivt.
Fältstudierna av biologisk mångfald visade att artrikedomens av växter, fåglar och fladdermöss ökar ju fler träd som finns på betesmarken. Däremot var andra vegetationsstrukturer i och runt betesmarkerna viktigare för den funktionella mångfalden. Frösåningsexperimentet påvisade hur effekten av träd på gräsmarksvegetation beror på just vilka arter av träd som finns där, vilket är intressant med tanke på brukarnas tendens att välja vilka trädarter som får vara kvar, samt att vissa arter faktiskt drar nytta av skuggning av träd under gröningsprocessen. Genom att analysera hur funktionell mångfald påverkas av vilka egenskaper hos respektive artgrupp som inkluderas i dessa analyser påverkar resultaten klargjordes på flera sätt hur funktionell mångfald inom de undersökta artgrupperna varierar. På så sätt kunde trädens och andra vegetationsstrukturers effekter på funktionell mångfald summeras i att växt- och fågelsamhällen påverkas främst genom hur de nyttjar resurser i form av näring och föda, medan fladdermöss påverkas mest i form av hur de rör sig genom vegetation (i sitt födosökande).

Avhandlingen visar att en begränsning av antal träd i betesmarker riskerar att förbise en rad olika biologiska värden av flera organismgrupper, men också på hur denna begränsning skapade konflikter mellan framförallt myndigheter och brukare. Trädregeln har därför på många olika plan bortsett från och missgynnat många av kopplingarna mellan kulturella och biologiska värden och den skötsel som skapat dessa värden. Dessa kopplingar bör inkluderas på ett bättre sett i regelverk som styr skötseln av jordbrukslandskapet i sin helhet och naturbetesmarker i synnerhet. Därför är det mycket lovande att EU i november 2017 öppnade upp för att inte längre fokusera på antal träd i betesmarkerna, liksom att Jordbruksverket i revideringar av sina riktlinjer framhäver värdena av träd för biologisk mångfald. Förhoppningsvis har denna avhandling bidragit till dessa förändringar, samtidigt som den bidrar till att fylla viktiga kunskapsluckor gällande effekter av träd i betesmarker på biologisk mångfald.
Rekommendationer för policy och skötsel av betesmarker

• Resultaten från denna avhandling visar att ju fler träd det finns på en betesmark, desto fler arter av växter, fåglar och fladdermös finns där. Det är dock viktigt att komma ihåg att artsammansättningen ser olika ut i marker med olika trädtäthet. För att bevara en hög biologisk mångfald på större skala i landskapet så är det viktigt att bibehålla variationen i trädtäthet mellan olika betesmarker.

• De positiva effekterna av träd på biologisk mångfald är ett resultat av lång kontinuitet av beteshävd, och ska inte förväxlas med ökad trädtäthet till följd av igenväxning. Fortsatt skötsel av trädbevarande betesmarker är av yttersta vikt för att bibehålla variation inom betesmarker och genom det bevara deras biologiska värden. På så sätt kan förhoppningsvis en del av homogeniseringen av jordbrukslandskapen motverkas och på så sätt gynna biologisk mångfald.

• Det här arbetet visar hur olika organismgrupper står för biologiska värden som inte nödvändigtvis hänger ihop, och därmed också påverkas på olika sätt av hur deras livsmiljö ser ut. Man bör därför ta mer hänsyn till flera olika organismgrupper när riktlinjer för skötsel av betesmarker bestäms för att säkerställa att viktiga ekologiska värden inte förbises.

• Analyserna av funktionell mångfald i trädbevarande betesmarker visar på komplexa förhållanden mellan arters egenskaper, den funktionella mångfalden och hur dessa påverkas av träd och andra strukturella attribut i betesmarker. Denna komplexitet motiverar mer forskning i ämnet, och jag vill uppmuntra att tills vidare använda enklare mått, t.ex. artrikedom, för att ge riktlinjer för skötsel av betesmarker.

• Trädbevarande betesmarker bär på en historia av beteshävd med stark koppling till kulturella traditioner, och deras värden är till stor del skapade av variation i skötsel. Det visar också resultaten från denna avhandling, där många brukare inte har ändrat sina skötselmetoder för att få de ersättningar som alltför hög trädtäthet har förhindrat. Dessutom har detta arbetet visat på många biologiska värden som är kopplade till andra vegetationssstrukturer än just antal träd. Därför behövs det mer flexibilitet i riktlinjer inom policy för att säkerställa att de många olika kultur- och naturvärdena som finns i trädbevarande betesmarker bevaras.

• Detta arbete visade också på hur brukare värderar träd med avseende på allt ifrån värden för boskap och biologisk mångfald till estetiska värden i landskapet. Intressant var också hur specifika trädarter tenderar att bevaras i betesmarker, vilket potentiellt har stora effekter på biologisk mångfald. Träd och dess värden utgör därför en potentiellt bra utgångspunkt för att på ett effektivt och lättförståeligt sätt diskutera skötsel av naturbeskapsmarker, så länge den kunskap som finns bland brukare och forskare gällande betesmarkers olika värden tas till vara.
Dissertation content

This doctoral compilation dissertation consists of a summarising text and the four articles listed below:


Author contributions

The author contributions for each paper in this thesis are divided as follows:

I M.S. conceived the ideas and designed the methodology together with S.J., M.S. collected and analysed the interview data. S.J. collected and analysed the biological data. M.S. led the writing and S.J. critically contributed to all versions of the manuscript.

II S.J. conceived the ideas and designed the methodology together with R.L., S.J. collected and analysed the data and led the writing of the manuscript. R.L. critically contributed to all versions of the manuscript.

III S.J. conceived the ideas and designed the methodology together with J.P. and R.L., S.J. collected and analysed the data and led the writing of the manuscript. All co-authors critically contributed to all versions of the manuscript.

IV S.J. conceived the ideas and designed the methodology together with H.W., J.E. and R.L. S.J. collected data on plant and bird communities, H.W. collected bat community data, S.J. analysed the data and led the writing of the manuscript. All co-authors critically contributed to all versions of the manuscript.
1 Introduction

One of the most important challenges within biodiversity conservation is to maintain high quality habitats within intensively managed landscapes, such as agricultural landscapes. In agriculture, landowners and farmers play key roles shaping the structure and composition of habitats. However, within the European Union (EU), farmers are strongly dependent on agricultural subsidies, which are guided through the Common Agricultural Policy (CAP). Therefore, policy regulations steering farmers’ management decisions form powerful tools to preserve high biodiversity values in agricultural landscapes.

Wooded pastures, pastures partly covered with trees, are among the most valuable habitats within an agricultural landscape context. They contribute to landscape level heterogeneity, a unique structurally complex habitat in itself and thus provide home to a wide range of organisms. Wooded pastures, as well as their biological values, are characterised by the presence of trees. Nevertheless, one focus point within the CAP regarding pasture management has restricted the number of trees that farmers are allowed to keep in their pastures to obtain agricultural support. This CAP regulation is based on an arbitrary limit with no solid evidence from the scientific literature.

Therefore, in this thesis, I investigate how tree density, and other vegetation attributes in wooded pastures, such as shrubs and structural complexity, affect biodiversity. To do so, I look at both the farmers’ perspective on policy guidelines and tree management as well as how trees affect biodiversity patterns across multiple biological taxa and what mechanisms that drive those pattern. The main objective is to better understand the farmers’ view on the tree density regulation and to provide scientific evidence of the effects of trees on biodiversity in wooded pastures. Through that, I aim to inform future policy guidelines to ensure maintained biological values of wooded pastures.

During the work with this thesis, the CAP has changed several times, also regarding the tree density regulation. Recently, in November 2017, the European Commission announced that they will reduce the focus on the number of trees that farmers are allowed to have in their pastures. First of all, I hope that the findings within this thesis have, to some extent, contributed to the knowledge basis for these changes. Secondly, the CAP changes frequently and updated scientific evidence regarding farmers’ situation and biodiversity patterns is needed for biodiversity conservation in agricultural landscapes in general and wooded pastures in particular.
2 Background

2.1 Changing agricultural landscapes, biodiversity and policy

The mosaic of habitats that low intensity agricultural management creates is essential for individual species and coexistence of species, with resulting high biodiversity at a landscape scale (Law and Dickman, 1998; Tscharntke et al., 2005; Billeter et al., 2008). Low-intensity agricultural management relies largely on the dependency on nature in farming practices (cf. Saltzman et al., 2011). However, the dependency shift from natural or semi-natural conditions to external inputs, e.g. nutrients, pesticides and water (Witcombe et al., 1996; Tilman et al., 2002), is part of the reason behind intensification and abandonment of low-intensively managed habitats (Vera, 2000; Billeter et al., 2008; Hartel and Plieninger, 2014), although regional-specific drivers may determine abandonment patterns (Beilin et al., 2014). Agricultural intensification and abandonment leads to habitat degradation and landscape simplification (Landis, 2017), which are among the most prominent human mediated global changes (Allan et al., 2015; Newbold et al., 2015) and major drivers of biodiversity loss (Pereira et al., 2012; Tscharntke et al., 2012; Queiroz et al., 2014; Gámez-Virués et al., 2015; Tsiafouli et al., 2015). Therefore, habitat and landscape heterogeneity are essential for biodiversity conservation and sustainability (Benton et al., 2003; Tews et al., 2004; Abson et al., 2013; Duru et al., 2015).

Policy guidelines form essential tools to mitigate the negative impacts of agricultural intensification and preserve biodiversity values in agricultural landscapes (Rands et al., 2010; Hodge et al., 2015; Rode et al., 2015). Indeed, the Common Agricultural Policy (CAP) within the European Union (EU) has a large impact on agricultural practices and land use (Benton et al., 2003; Hodge et al., 2015), with 38% of the total EU budget dedicated to agricultural subsidies (European Commission, 2017b). The large monetary input from the EU makes farmers highly dependent on subsidies for profitability in farming (Roellig et al., 2016), although the dependency on EU subsidies varies across Europe (European Commission, 2017a). As farmers are the ultimate managers of agricultural land and essential food producers, they play a key role to preserve biodiversity values in parallel with a sustainable food production. However, without steering policy guidelines, those goals might not be reached due to high costs of continued management or lack of motivation to manage the land (Rode et al., 2015; Raatikainen and Barron, 2017).

At a global scale, the communication of scientific evidence often fails to reach policymakers (Bainbridge, 2014; Rose, 2015), which results in a large information gap between policy and biodiversity conservation (Geijzendorffer et al., 2015). Such a mismatch is part of the reason why the EU through the CAP has repeatedly failed to mitigate the negative impacts from land use abandonment and intensification on biodiversity (Hodge et al., 2015). Although targeted applied research is needed (Beaufoy and Marsden, 2011; Plieninger et al., 2015), it may be even more important to bridge the gap between science,
policy and management as the perception of the values of biodiversity itself may differ both between geographical regions and between different stakeholders, e.g. farmers and policy makers (Herzon and Mikk, 2007; Cáceres et al., 2015; Plieninger et al., 2015). In particular, the vast experience based knowledge among farmers needs to be considered to assess the social-ecological values of habitats and habitat features (Barton et al., 2016; Raatikainen and Barron, 2017). Hence, to better understand differences in perceptions and how those affect biodiversity, it is important to investigate the link from policy to biodiversity through land managers (Mattison and Norris, 2005).

Variation in climate, topography and management traditions make the EU a very heterogeneous policy arena. Instead of being a social-political border that dissects ecological boundaries (e.g. Cousins et al., 2014; Dallimer and Strange, 2015), the EU could be seen as a social-political border that encompasses social-ecological system boundaries. Inevitably, the CAP thus drives homogenisation of diverse systems through categorical boundaries (cf. Dahlberg, 2015) into either forests or arable lands, with large negative impacts on biodiversity (Benton et al., 2003; King, 2010; Beaufoy et al., 2011). Agriculture and forest are two distinct land-use categories guided by separate governing bodies and management rationales (Hartel and Plieninger, 2014; Stenseke et al., 2016), where agricultural policy falls under the regulations of the EU, whereas forestry is controlled mainly by national governance.

In the middle of this ongoing landscape homogenisation and governmental polarisation, semi-natural wooded pastures, with trees but under agricultural management, have become stuck in a dichotomy between agriculture and forestry (Beaufoy, 2014; Plieninger et al., 2015; Roellig et al., 2016). Particularly alarming for wooded pasture management and biodiversity, the EU in 2003 introduced a tree density regulation within the CAP (implemented in different years in different countries). The regulation limited the number of trees that farmers were allowed to have in their pastures to receive Direct Payment subsidies from the EU (Beaufoy et al., 2011). The social-ecological link in wooded pasture management (Fischer et al., 2012) suggests that these habitats may be particularly sensitive to such specific policy directives (see also Rode et al., 2015; Beaufoy et al., 2015; Plieninger et al., 2015). Therefore, targeted research is needed in order to improve the knowledge about farmers’ decisions and better understand how policy guidelines affect management of wooded pastures and their biodiversity values.

2.2 Wooded pastures – characterisation, values and policy

Characterisation

Within Europe, wooded pastures constitute a variety of grazed grasslands with trees, covering approximately 200 000 km² of land (Plieninger et al., 2015). They can be very open with just a few trees, semi-open single tree species dominated pastures to relatively dense grazed woodlands (Figure 2.1; Bergmeier et al., 2010; Plieninger et al., 2015), with large tree density variations both between and within regions (Hartel and Plieninger, 2014). Continuous grazing and the presence of trees and shrubs have created heterogeneous habitats (Bakker et al., 2004; Dufour et al., 2006; Peringer et al., 2017), with high biodiversity values both within the pastures (Babai and Molnár, 2014; Hartel and Plieninger, 2014; Oldén et al., 2016) and in a landscape context (Billeter et al., 2008; Rossi et al., 2016; Wood et al., 2017).
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Social and ecological values

The historical importance of wooded pastures for humans all over Europe (Holl and Smith, 2002; Sjögren, 2006; Albery, 2011) contributes to a wide variety of sociocultural values such as aesthetics, recreation, cultural heritage and preservation of traditional knowledge (see Plieninger et al. (2015) for a review). Interestingly, these social values may be strongly attached to trees (Blicharska and Mikusiński, 2014), which also support many biodiversity values (Manning et al., 2006; Prevedello et al., 2017). The presence of old-growth trees and long continuity of low-intensity management create biodiversity values that stretches across many different taxa (Fischer et al., 2010; Bugalho et al., 2011; Moreno et al., 2016). In the otherwise homogenised agricultural landscapes of Europe, wooded pastures are therefore essential for biodiversity conservation (Dicks et al., 2014). Within pastures, trees have positive effects on many ecological functions and are therefore keystone features for biodiversity at local and landscape scales (Manning et al., 2006; Rossi et al., 2016). Besides the benefits for biodiversity, wooded pastures and other silvo-pastoral systems generally contribute to society through multiple processes, such as productivity, soil fertility and soil stability, which are linked to trees within the pastures (Barton et al., 2016; Torralba et al., 2016; García de Jalón et al., 2018). These links indicate a close relationship between trees, biodiversity and food production potential in wooded pastures, valuable for sustainable agricultural practices (Smith et al., 2012; Oppermann, 2014; Barrios et al., 2017).

Wooded pastures and policy

Despite their high social-ecological values, wooded pastures face an uncertain future due to abandonment, land use intensification and lack of emphasis within policy guidelines (Beaufoy et al., 2015; Plieninger et al., 2015). As trees form major drivers of both social and ecological values (Manning et al., 2006; Blicharska and Mikusiński, 2014; Hartel et al., 2017), one of the major obstacles for continued wooded pasture management could be the tree density regulation within the CAP. The limit was first set to 50 trees/ha, increased to 100 trees/ha in 2014 (European Commission, 2014) and recently the EU indicated that the tree density focus will be removed from the CAP regulations (European Commission, 2017c). Although limiting the number of trees in pastures certainly keeps the pastures and the agricultural landscapes open, this limit seems arbitrary and exemplifies simplification of nature and categorical policy guidelines where heterogeneity within and between habitats does not fit (Scott, 1998; Dahlberg, 2015).
The tree density regulation has neglected the values of trees as important features in pastures, shaping plant and animal communities (see Section 2.4). The regulation has also resulted in large scale abandonment of wooded pastures (Hartel and Plieninger, 2014), with negative impacts on biodiversity (e.g. Pykälä et al., 2005; Dahlström et al., 2010; Oldén et al., 2016). Although many studies suggest that increased tree cover as a result of abandonment has negative effects on biodiversity (e.g. Öckinger et al., 2006; Bugalho et al., 2011; Oldén et al., 2016), few studies have specifically looked at the effects of tree density on biodiversity along a tree density gradient from very open to very dense pastures that are continuously managed (but see Catarino et al., 2016 and Caruso et al., 2015). Besides the scarce scientific evidence from complete tree density gradients in continuously managed pastures, effects of tree cover may vary depending on the type of tree cover (or habitat) that is studied (Harvey et al., 2006), which emphasises how results from other wooded habitats cannot be translated into ecological processes in wooded pastures. Thus, the potential impact of regulating tree numbers of continuously managed wooded pastures needs to be investigated to adopt policies for preserving their high biological values.

2.3 Biodiversity – values and metrics

The need for biodiversity for a sustainable future, also for humans, has been repeatedly emphasised in the scientific literature (Cardinale et al., 2012; Díaz et al., 2018). Biodiversity is a prerequisite for ecosystem functioning (Duffy et al., 2007; Pasari et al., 2013; Tilman et al., 2014; Lefcheck et al., 2015) and acts as an insurance mechanism for society (Baumgärtner, 2007; Craven et al., 2016). Biodiversity is the variability among living organisms, and could relate to any set of organisms at any spatial, temporal and biological scale (Purvis and Hector, 2000). Species richness – the number of species of a group of organisms – is the most commonly used measure of biodiversity, hence also widely used in conservation strategies (Purvis and Hector, 2000; Gotelli and Colwell, 2001). However, due to its simplicity, species richness may not be suitable to estimate effects of land use changes or targeted environmental schemes (Ekroos et al., 2014; Batáry et al., 2015; Valiente-Banuet et al., 2015).

Scale-related metrics such as beta diversity, reflecting species turnover between locations (Tuomisto, 2010; Chiarucci et al., 2011), may be more relevant in a biodiversity conservation context (Socolar et al., 2016). However, a functional approach might be required to better understand why biotic communities differ in relation to environmental conditions (Petchey and Gaston, 2002; Cadotte et al., 2011). Compared to species richness, functional diversity is a better predictor of ecosystem functioning (Gagic et al., 2015; Finney and Kaye, 2017). Functionally diverse communities are therefore more likely to adapt to changes in the environment, including anthropogenic pressures (Chillo et al., 2011). Functional diversity may be especially relevant to inform policies targeting social-ecological systems such as wooded pastures where the pastures’ contribution to society is important (Oppermann, 2014; Laurila-Pant et al., 2015).

Choice of biodiversity measures in this thesis

Vascular plant communities are commonly used as indicators of habitat quality and for estimations of best management practices of grasslands (e.g. Gaujour et al., 2012; Socher et al., 2013; Dengler et al., 2014; Minden et al., 2016; Tälle et al., 2016). This is in line with policy strivings for simplicity (Purvis and Hector, 2000; Ekroos et al., 2014), but
the biological values of wooded pastures stretch beyond plant communities (Fischer et al., 2010; Moreno et al., 2016; Torralba et al., 2016) and many organism groups are particularly dependent on the presence of trees (Manning et al., 2006; Fischer et al., 2010; Harvey et al., 2011; Prevedello et al., 2017). Dissimilarities between different taxa, their responses to the environment and their effects on ecosystem functioning motivate studies on multiple taxa to inform policy guidelines (Pärt and Söderström, 1999a; Billeter et al., 2008; Pedley and Dolman, 2014; Eglington et al., 2015; Lefcheck et al., 2015). Convincing policy-makers about multiple biodiversity values, stretching beyond simple species richness measures of one taxon is a key task for ecologists (Purvis and Hector, 2000). Although a number of recent studies have taken a multiple taxa approach (e.g. Aubin et al., 2013; Pedley and Dolman, 2014; Jonason et al., 2017), none of them focused on the structure of pastures in general and tree density in particular.

Thus, besides investigating vascular plant communities, this thesis also looks at bat and bird communities, two groups rarely used as indicators of pasture quality. In contrast to plants, bats and birds are mobile organisms that are expected to respond quicker to environmental changes (Aubin et al., 2013; Roth et al., 2014), hence also showing different assets of biodiversity (e.g. Pärt and Söderström, 1999a; Manning et al., 2015). Responses of bats and birds to environmental differences are also expected to differ, as bat species in Sweden are predominantly insectivorous whereas the bird communities represent a wider food resource range. For a better representation of ecosystem functioning (cf. Gagic et al., 2015 and Finney and Kaye, 2017), the thesis also takes a functional approach on pasture biodiversity patterns.

2.4 Effects of trees on plants, birds and bats

The following section summarises the existing literature on the effects of trees on plants, birds and bats, and extends briefly to effects of other vegetation characteristics. Concerning the effects of tree density on the diversity of these taxa, there are indications that tree density may have a positive impact on all of them. However, there is no solid scientific evidence from large tree density gradients in continuously managed pastures, in particular regarding effects on functional diversity. Among the studies targeting a large tree density gradient in managed pastures, most have been published contemporary to this thesis (Table 2.1).

**Plants**

Trees affect the abiotic conditions determining plant community patterns, such as light, water and nutrient conditions (Joffre et al., 1993; Barbier et al., 2008; Holdo and Mack, 2014). Competition for these resources may have a negative impact on plant species diversity through competitive exclusion (Hardin, 1960; Newman, 1973; Grime, 2006; Abdallah and Chaieb, 2012). Although solitary trees have positive impacts on plant diversity (Manning et al., 2006; Kiebacher et al., 2017), high tree densities may turn this into a negative effect (e.g. Gillet et al., 1999 and Rolo et al., 2016). However, grazing has a general independent positive effect on plant diversity (Ejrnæs and Bruun, 1995) and long continuity of low intensity management is a major driver of grassland plant diversity (Cousins and Eriksson, 2002; Aavik et al., 2008). Thus, long time low-intensity grazing potentially removes the negative effects of trees on grassland communities, but could have different effects on taxonomic and functional diversity (Table 2.1). Canopy shading of different tree species may have different effects on the plant communities be-
neath them due to species-specific effects on soil conditions (Vesterdal et al., 2008; Cools et al., 2014; Soliveres et al., 2015). Species-specific effects of trees on plant communities can appear already at the germination stage of plant communities (Bruun and Ten Brink, 2008; Thomaes et al., 2011), related to species’ habitat preferences (Vandelook et al., 2008). Hence, trees may be key ecosystem engineers (Jones et al., 1994) in shaping plant communities at several stages of plant life cycles. However, studies on the effects of tree species on grassland plant communities are not well represented in the scientific literature, where forest understory commonly is the target plant community.

**Birds**

Trees, and other vegetation structures in open landscapes, are known to have a large impact on bird communities (Hodgkison et al., 2004; Cunningham and Johnson, 2006; Hodgkison et al., 2007; Ikin et al., 2012). Tree canopies are used by birds for nesting, foraging and shelter (e.g. Dean et al., 1999; Fischer and Lindenmayer, 2002; Luck and Daily, 2003). Cavities in trees are also important nesting sites for birds (e.g. Dean et al., 1999; Manning et al., 2004). Hence, tree density could be expected to have positive effects on bird species richness. Indeed, some studies have shown that the number of bird species increases with increasing tree densities, but few have included very dense pastures (Table 2.1). However, results from studies of wooded pastures as well as how birds use scattered trees suggest a functional response of birds to tree structure, size and landscape context (Fischer and Lindenmayer, 2002; Hartel et al., 2014), which results in guild-specific effects of trees on species richness patterns (e.g. Catarino et al., 2016). However, due to the effects of grazing on bird communities (Laiolo et al., 2004), different patterns may appear when studying tree density gradients in continuously grazed grasslands compared to other wooded habitats. Until now, Catarino et al. (2016) and Jakobsson and Lindborg (2017) are the only studies targeting an almost complete tree density gradient in grazed pastures (Table 2.1).

**Bats**

Bats are in general dependent on additional vegetation features that increase habitat heterogeneity and complexity, driven by the positive correlation with prey abundance (Lentini et al., 2012; Müller et al., 2012). Similar to birds, bats benefit from the presence of trees in multiple ways, e.g. using them as roosting sites and foraging substrates (Law et al., 2000; Lumsden and Bennett, 2005; Silvis et al., 2015; Le Roux et al., 2018). Therefore, several studies have shown a positive impact of tree density on bat activity and species richness (Table 2.1), although species richness may saturate at just a few trees/ha in open areas (Fischer et al., 2010). However, Wood et al. (2017) is the only study that has targeted continuously managed wooded pastures covering the range of tree densities common in some European countries, such as Sweden. Even less is known about the functional responses of bat communities to tree density at habitat scale (Table 2.1), which is likely to be important due to bats’ dependency on the presence of trees and other vegetation structures, especially for foraging (Loeb and O’Keefe, 2006; Manning et al., 2006; Rainho et al., 2010; Jung et al., 2012).
Table 2.1. Compilation of the scientific literature on the effects of tree density/cover on taxonomic and functional diversity of plants, birds and bats in managed grasslands (for bats also activity). Effects are briefly described as significantly positive (+), negative (-), polynomial (⌢) or no significant effect (n.s.). For details, see references. This compilation is not a result of a complete systematic literature search, but summarises published literature cited in this thesis.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Reference</th>
<th>Response variable</th>
<th>Explanatory variable</th>
<th>Range or Comparison</th>
<th>Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plants</td>
<td>Aavik et al. (2008)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Total richness</td>
<td>irradiation (%)</td>
<td>20–90</td>
<td>n.s.</td>
</tr>
<tr>
<td></td>
<td>Caruso et al. (2015)</td>
<td>Total richness</td>
<td>canopy cover (%)</td>
<td>3–210</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Caruso et al. (2015)</td>
<td>- pasture specialists</td>
<td>trees/ha</td>
<td>3–210</td>
<td>n.s.</td>
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<td></td>
<td></td>
<td>Specialist richness</td>
<td>trees/ha</td>
<td>3–210</td>
<td>n.s.</td>
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<td></td>
<td></td>
<td>- pasture specialists</td>
<td>trees/ha</td>
<td>3–210</td>
<td>n.s.</td>
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<td></td>
<td>Dorrough et al. (2006)</td>
<td>Total richness&lt;sup&gt;b&lt;/sup&gt;</td>
<td>canopy cover (%)</td>
<td>0–100</td>
<td>+</td>
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<td></td>
<td></td>
<td>Total richness&lt;sup&gt;c&lt;/sup&gt;</td>
<td>canopy cover (%)</td>
<td>0–100</td>
<td>n.s.</td>
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<td></td>
<td>Gillet et al. (1999)</td>
<td>Total richness&lt;sup&gt;d&lt;/sup&gt;</td>
<td>canopy cover (%)</td>
<td>0–100</td>
<td>n.s.</td>
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<td></td>
<td>Oldén et al. (2016)</td>
<td>Total richness</td>
<td>trees/ha</td>
<td>0–70</td>
<td>⌄</td>
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<td></td>
<td></td>
<td>Functional dispersion</td>
<td>woody cover (%)</td>
<td>0–90</td>
<td>⌄</td>
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<td></td>
<td></td>
<td>Shöderström et al. (2001)</td>
<td>tree cover (%)</td>
<td>0–54.3</td>
<td>n.s.</td>
</tr>
<tr>
<td>Birds</td>
<td>Catarino et al. (2016)</td>
<td>Total richness</td>
<td>tree cover (%)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>10–80</td>
<td>n.s.</td>
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<tr>
<td></td>
<td></td>
<td>- farmland species</td>
<td>tree cover (%)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>10–80</td>
<td>-</td>
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<td></td>
<td></td>
<td>- edge species</td>
<td>tree cover (%)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>10–80</td>
<td>n.s.</td>
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<td></td>
<td></td>
<td>- forest generalists</td>
<td>tree cover (%)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>10–80</td>
<td>+</td>
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<td></td>
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<td>- forest specialists</td>
<td>tree cover (%)&lt;sup&gt;e&lt;/sup&gt;</td>
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<td></td>
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<td>- conservation status</td>
<td>tree cover (%)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>10–80</td>
<td>-</td>
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<tr>
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<td>Total richness</td>
<td>trees/ha</td>
<td>0–59</td>
<td>+</td>
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<tr>
<td></td>
<td>Harvey et al. (2006)</td>
<td>Total richness</td>
<td>high vs. low&lt;sup&gt;h&lt;/sup&gt; (%)</td>
<td>0–5 vs. 16–25</td>
<td>+</td>
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<td></td>
<td></td>
<td>- frugivorous</td>
<td>high vs. low&lt;sup&gt;h&lt;/sup&gt; (%)</td>
<td>0–5 vs. 16–25</td>
<td>n.s.</td>
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<td></td>
<td>Jakobsson and Lindborg (2017)&lt;sup&gt;i&lt;/sup&gt;</td>
<td>Total richness</td>
<td>trees/ha</td>
<td>3–214</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Söderström et al. (2001)</td>
<td>Total richness</td>
<td>tree cover (%)</td>
<td>0–54.3</td>
<td>n.s.</td>
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<td></td>
<td>Tellería (2001)</td>
<td>Total richness</td>
<td>trees/ha</td>
<td>0–100</td>
<td>-</td>
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<td></td>
<td></td>
<td>- arboreal species</td>
<td>trees/ha</td>
<td>0–400&lt;sup&gt;j&lt;/sup&gt;</td>
<td>+</td>
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<td></td>
<td></td>
<td>- border species</td>
<td>trees/ha</td>
<td>0–400&lt;sup&gt;j&lt;/sup&gt;</td>
<td>-</td>
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<tr>
<td>Bats</td>
<td>Fischer et al. (2010)</td>
<td>Total richness</td>
<td>trees/ha</td>
<td>0–100</td>
<td>+</td>
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<tr>
<td></td>
<td>Harvey et al. (2006)</td>
<td>Total richness</td>
<td>high vs. low&lt;sup&gt;h&lt;/sup&gt; (%)</td>
<td>0–5 vs. 16–25</td>
<td>n.s.</td>
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<td></td>
<td>Kalda et al. (2015)&lt;sup&gt;k&lt;/sup&gt;</td>
<td>Total richness</td>
<td>trees/ha</td>
<td>1–300&lt;sup&gt;j&lt;/sup&gt;</td>
<td>+</td>
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<td></td>
<td></td>
<td>Total activity</td>
<td>trees/ha</td>
<td>1–300&lt;sup&gt;j&lt;/sup&gt;</td>
<td>+</td>
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<td></td>
<td>Lumsden and Bennett (2005)&lt;sup&gt;k&lt;/sup&gt;</td>
<td>Total activity</td>
<td>trees/ha</td>
<td>0–34/300&lt;sup&gt;m&lt;/sup&gt;</td>
<td>+ / ⌄</td>
</tr>
<tr>
<td></td>
<td>Wood et al. (2017)&lt;sup&gt;k&lt;/sup&gt;</td>
<td>Total richness</td>
<td>trees/ha</td>
<td>3–214</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total activity</td>
<td>trees/ha</td>
<td>3–214</td>
<td>⌄</td>
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<td></td>
<td></td>
<td>- forest specialists</td>
<td>trees/ha</td>
<td>3–214</td>
<td>⌄</td>
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<td></td>
<td></td>
<td>- interface specialists</td>
<td>trees/ha</td>
<td>3–214</td>
<td>⌄</td>
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<td></td>
<td></td>
<td>- open specialists</td>
<td>trees/ha</td>
<td>3–214</td>
<td>⌄</td>
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<tr>
<td></td>
<td></td>
<td>Feeding activity</td>
<td>trees/ha</td>
<td>3–214</td>
<td>⌄</td>
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</tbody>
</table>

<sup>a</sup> Wooded meadows; <sup>b</sup> Light and intermittent grazing pressure; <sup>c</sup> Heavy grazing pressure; <sup>d</sup> Tree density used in analyses, figures show basal area (m²/ha); <sup>e</sup> Experimental fire management of a grassland–woodland ecotone; <sup>f</sup> Mean dissimilarity between sub-plots; <sup>g</sup> Analysis on tree density, but visualisation of variation is on tree cover; <sup>h</sup> Comparison between pastures with either 0–5 or 16–25% tree cover; <sup>i</sup> Studies from which data are used in this thesis; <sup>j</sup> Including broadleaved and conifer woodlands (wooded pastures up to 100 trees/ha); <sup>k</sup> Trees in agricultural landscapes; <sup>l</sup> Range from solitary trees to tree lines to woodlands; <sup>m</sup> Scattered tree gradient up to 34 trees/ha, higher tree densities represented by remnant woodland blocks.
3 Aims and Scopes

The lack of evidence-based policy-making is an urgent issue for effective biodiversity conservation, especially for wooded pastures. There are still substantial knowledge gaps regarding how trees in pastures affect biodiversity, especially concerning the functional responses across multiple taxa. The overarching aim of this thesis is therefore to investigate how the CAP tree density limitation affects wooded pasture management and how tree density affects wooded pasture biodiversity values. Farmers’ perspective on management, trees and biodiversity is used as an entry point, after which targeted field studies on biological communities are used to answer how biodiversity is affected by trees and other structural attributes of wooded pastures (Figure 3.1).

Figure 3.1. Thesis overview. Box colours represent different papers in the thesis, filled arrows show relationships studied, hollow arrows show relationships not included in the thesis, grey lines show sub-categories linked to main topics. a = tree density and other pasture vegetation attributes.
3.1 Objectives

The specific objectives of this thesis are to:

A) Improve the understanding of farmers’ view on the CAP tree density limitation and how farmers potentially adapt to this regulation

**Motivation:** To understand management effects on biodiversity and ultimately to inform policy guidelines it is crucial to include also farmers’ perspective on the system. Several studies have already highlighted farmers’ appreciation of pasture trees but the perceptions of biodiversity values vary between regions and stakeholders. Thus, understanding farmers in the studied region is essential to inform policy directives, especially concerning social-ecological systems such as wooded pastures.

B) Investigate how taxonomic and functional biodiversity are affected by tree density along a complete tree density gradient in managed wooded pastures with long management continuity

**Motivation:** Although a number of studies have investigated the effects of trees on biodiversity, very few have targeted the range of tree densities found in many European pasture systems. Thus, there is no clear consensus about these effects, and even less is known about the functional responses to tree density, which is key to understanding the effects of trees on ecosystem functioning.

C) Increase the mechanistic understanding of biodiversity responses of multiple taxa in relation to trees in wooded pastures

**Motivation:** Studies on taxonomic and functional diversity patterns tend to lack deeper analytical approaches to understand those patterns. Therefore, to clarify the biodiversity patterns found and make the results more transparent, approaches to increase the mechanistic understanding of biodiversity are needed.

The objectives are addressed in Papers I-IV through an interview study, field data collection and analyses of different predictor and response variables (Table 3.1; Figure 3.1).

Table 3.1. Overview of the studies included in this thesis: how they relate to the specific objectives and brief method descriptions.

<table>
<thead>
<tr>
<th>Paper</th>
<th>Objective</th>
<th>General method</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>A</td>
<td>Interview study with farmers to investigate their view on CAP and management of pasture trees</td>
</tr>
<tr>
<td>II</td>
<td>B &amp; C</td>
<td>Field study on plant diversity and species composition in relation to trees</td>
</tr>
<tr>
<td>III</td>
<td>C</td>
<td>Field experiment on plant species’ germination responses in relation to different tree species</td>
</tr>
<tr>
<td>IV</td>
<td>B &amp; C</td>
<td>Field study on taxonomic and functional diversity of multiple taxa in relation to trees</td>
</tr>
</tbody>
</table>
4 Methods

4.1 Study area

This thesis has been conducted within the UNESCO biosphere reserve Östra Vätterbranterna in southern Sweden (Figure 4.1). In 2012, this area was designated a biosphere reserve, in which social and ecological systems are linked to ensure a sustainable use of the reserve and with that preserve biodiversity (UNESCO, 2015). The biosphere reserve, covering approximately 70,000 ha, is characterised by a mosaic landscape structure, relatively rich in small scale farming and semi-natural wooded pastures. Hence, it is a representative area of a relatively low-intensively managed Swedish landscape mosaic, in contrast to the agricultural plains in other parts of southern Sweden. The topographical complexity and its glacial origin split the landscape in arable fields in the lowlands on fertile glacial-fluvial deposits and forest dominated hills on shallow soils, rich in bedrock outcrops. Wooded pastures are typically found on the hillsides, forming intermediate habitats between arable fields and forests (Jakobsson and Lindborg, 2014).

Figure 4.1. Study sites within the biosphere reserve Östra Vätterbranterna in southern Sweden. Modified from Paper II.
The policy situation in Sweden

In Sweden, the tree density regulation was implemented in 2008 and initially caused conflicts between Sweden and the EU (Blom, 2010). However, Sweden was eventually allowed to adjust the first limit of 50 trees/ha to 60 trees/ha in general and to 100 trees/ha for pastures with high biological and/or cultural values concerning the Direct Payment Scheme (part of the CAP Pillar I) (Beaufoy et al., 2011). Above that limit, the Rural Development Scheme (CAP Pillar II) has compensated highly valued pastures, subsidised both by the EU and Sweden. With the new subsidy guidelines in 2014, Sweden introduced even more flexible rules and recommendations regarding trees, encouraging farmers to keep trees of special character and high biological values (e.g. old-growth trees and trees with fleshy fruits) (Jordbruksverket, 2017a). In the regulations regarding Direct Payments, the Swedish Board of Agriculture emphasises the difference between trees and shrubs that are of overgrowth character and those that are not (Jordbruksverket, 2017b). The recent announcement from the EU to reduce the tree density focus in the regulations makes upcoming changes likely and hence scientific evidence is needed to inform pasture management guidelines.

Selection and characterisation of study sites

In order to meet the objectives of this thesis, I selected 64 semi-natural wooded pastures within the study area to cover a gradient of almost completely open pastures (just a few trees/ha) to very dense pastures (>200 trees/ha). These 64 pastures were used as baseline study sites, of which all were used in Paper II, whereas a subset of four pastures were used in Paper III and 21 pastures were used in Paper IV. In Paper I, only farmers owning or managing one or several out of the 64 pastures were interviewed. Pasture locations
and status were preliminary checked using the national database on agricultural lands in combination with satellite images (Google, 2013; Jordbruksverket, 2013). I used five pre-defined criteria regarding pasture status for final study selection in the field: 1) continuously grazed by livestock, 2) not recently and extensively cleared from trees, 3) having a relatively homogeneous (area of) tree cover, 4) on dry to semi-dry soil and 5) characterised of a forb/grass dominated field layer. To use comparative pastures (cf. Caruso et al., 2015), the study site selection considered only pastures of high nature values (Sw: speciella värden; defined by the County Administrative Board (Sw: Länsstyrelsen)), thus with an upper limit of 100 trees/ha to receive Direct Payment subsidies at the time of data collection for this thesis.

4.2 Data collection

*Interviews with farmers (Paper I)*

To investigate how farmers perceive pasture management in general and pasture trees in particular, semi-structured interviews were conducted with 22 farmers, 17 men and five women. The interviewed farmers, representing 17 different farms, own or manage pastures that were used to assess plant, bird and bat diversity (see below). They also represent a variety of farms, ranging from 25 to 400 ha in size and focusing on either dairy or meat production. Hence, the interviewed farmers were considered to represent the variety of farms and farmers in the study area. Farmers were asked questions about their background, farming conditions, how they look at wooded pasture management in general and how they manage trees specifically. Further, they were asked how the CAP affects management (in general and through the specific tree density limitation), their interest in biodiversity conservation issues and how pasture management relates to forest management (most farmers also own and manage forest). In addition to the interviews with farmers, two officials at the County Administrative Board and one at the Swedish Board of Agriculture (Sw: Jordbruksverket) were interviewed regarding CAP, guidance in relation to the CAP implementation and their perception of the farmers’ perspective. However, the focus in this thesis is the farmers’ perspective and therefore the results from those latter interviews are only discussed briefly.

*Explanatory variables (Paper I-IV)*

I estimated the structural characteristics of each wooded pasture by identifying and measuring (diameter at breast height (DBH), at 1.3 m) all individual trees and shrubs present within a representative subset of 0.8–1.4 ha of each pasture, hereafter referred to as a site. Using these data, it was possible to get a quick but detailed characterisation of the study sites using six local environmental variables: *tree density, shrub density, structural complexity, tree diversity* (Shannon diversity index H’ (Shannon, 1948)) and *tree species composition* (two variables). The latter, *tree species composition*, was estimated by extracting the first two axes from a Principal Component Analysis (PCA) on the tree species composition. In addition, I used aerial photos (Lantmäteriet, 2015) to estimate *proximate forest cover*. Details on variable calculations and how they were used are given in Table 4.1.

Although the focus of the thesis is on trees, I selected explanatory variables to cover a range of potential additional vegetation attributes which are likely to affect the studied biological communities. For example, understory vegetation has been shown to have a negative impact on bat species richness (Kalda et al., 2015) but a positive effect on bird
species richness (Laiolo et al., 2004), which links to how shrub density positively affects bird species richness (Pärt and Söderström, 1999b; Söderström et al., 2001). Habitat complexity may have positive impacts on birds but not plants (Eglington et al., 2015; Lengyel et al., 2016), whereas it affects both plant and bird species composition (Hovick et al., 2014; Myers et al., 2015; Lindgren et al., 2018). Landscape structure is known to have a large impact on local grassland plant diversity and species composition, but also influences bat and bird communities (e.g. Lindborg, 2007; Gazol et al., 2012; Reitalu et al., 2012; Schmucki et al., 2012; Tscharntke et al., 2012; Frey-Ehrenbold et al., 2013; Sánchez-Oliver et al., 2014; Charbonnier et al., 2016a; Le Roux et al., 2018). Concerning birds and bats, there are particularly clear functional responses to the surrounding landscape. For example, bat wing morphology and foraging strategy have been shown to relate to landscape openness (Cisneros et al., 2015). Mobility traits among birds also respond to habitat filtering related to vegetation cover (Trisos et al., 2014), and diversified agricultural landscapes in general have positive impacts on bird taxonomic and functional diversity (Fischer et al., 2011; Karp et al., 2012; Lee and Martin, 2017).

To estimate canopy cover, I took two photos vertically upward from each vegetation sampling plot (see below), using a fish-eye adapter lens (180°; the two photos 90° rotated to each other) for iPhone 4S. Canopy cover was used to estimate how tree densities were related to canopy cover (Paper II) and to analyse species-specific responses of plants (Paper III). I also divided the pastures into categories based on tree density in order to estimate potential effects of subsidy regulations based on specific tree densities (Paper II). The categories relate to the tree density limitations implemented by the EU over the last decade: 1) former CAP (0-50 trees/ha), 2) updated CAP (50-100 trees/ha) and 3) newest CAP/no limit (>100 trees/ha). These limits were different by the time these analyses were conducted, thus the categories were named differently in Paper II.

To control for the effects of soil conditions on plant communities (e.g. Ejrnæs and Bruun, 1995; Oldén et al., 2016), I took soil samples parallel to the plant inventories. Within each sampled plot for plant community assessment (see below), three top soil cores were extracted with a soil auger. The three sub-samples were mixed and left to air dry in room temperature. Prior to analysis, I ground and sieved the soil samples (for some analyses also homogenised, see Paper II for details). From the soil samples, soil pH, organic content, total carbon (C) and nitrogen (N) content and C:N-ratio were estimated. The soil variables were used in the analyses of Paper II and for site selection in Paper III.

This thesis ignores more detailed analyses of how spatial and temporal landscape configuration affect biodiversity patterns (Lindborg and Eriksson, 2004; Tscharntke et al., 2012; Birkhofer et al., 2018) as landscape scale regulations are rarely implemented in policy guidelines (Kleijn et al., 2006). However, local habitat characteristics in general filter biological communities (Zobel et al., 1998), have major influence on multi-functionality (Allan et al., 2014, 2015) and are easier to manage in practice compared to landscape-wide characteristics. To keep the study directly applied to policy, I therefore decided to focus on a habitat scale throughout the thesis.

Assessment of biological communities (Paper II-IV)
Within all 64 wooded pastures, I inventoried plant communities between 17 June and 3 August 2013. In each pasture, ten 1 m² sample plots where randomly placed within the pasture, in which the presence of each vascular plant species was recorded (Figure 4.3).
Wooded or treeless pastures?

Table 4.1. Explanatory variables used to characterise wooded pasture structure, the proximate land cover and soil properties. The papers in which each variable was included are defined in the right column, paper numbers in brackets means that the variable was not used in analysis but for a qualitative description. SD = standard deviation, DBH = diameter at breast height, PC = principal component. The seed sowing experiment variables (Paper III) are not included in the table.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Specification</th>
<th>Used in paper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree density</td>
<td>trees/ha</td>
<td>within pasture subset; trees with DBH &gt;10 cm</td>
<td>II, IV</td>
</tr>
<tr>
<td>Shrub density</td>
<td>shrubs/ha</td>
<td>within pasture subset</td>
<td>II, III, IV</td>
</tr>
<tr>
<td>Tree diversity</td>
<td>Shannon diversity H'</td>
<td>within pasture subset</td>
<td>II</td>
</tr>
<tr>
<td>Structural complexity</td>
<td>SD of DBH</td>
<td>within pasture subset</td>
<td>II, IV</td>
</tr>
<tr>
<td>Tree species composition</td>
<td>PC1/PC2</td>
<td>within pasture subset</td>
<td>II, III</td>
</tr>
<tr>
<td>Proximate forest cover</td>
<td>proportion of forest</td>
<td>within 250 m from centre</td>
<td>II, IV</td>
</tr>
<tr>
<td>Canopy cover</td>
<td>% canopy cover</td>
<td>above each plant sampling plot</td>
<td>III, (II)</td>
</tr>
<tr>
<td>Soil pH</td>
<td>pHKCl</td>
<td>each plant sampling plot</td>
<td>II, (III)</td>
</tr>
<tr>
<td>Soil organic content</td>
<td>% (loss on ignition)</td>
<td>each plant sampling plot</td>
<td>II, (III)</td>
</tr>
<tr>
<td>Soil C:N-ratio</td>
<td>C:N (combustion)</td>
<td>each plant sampling plot</td>
<td>II, (III)</td>
</tr>
</tbody>
</table>

Within 21 out of the 64 wooded pastures, I surveyed bird communities using point counts within the first four hours after sunrise, visiting every site five times between 22 April and 15 June 2014. During all visits, each site was surveyed for five minutes from the central point of the pasture and during an additional five minute slow walk circulating the site. All birds seen or heard within the site were recorded (Figure 4.3). I chose the point count approach because of the relatively small pastures sampled, for which five minutes has been suggested to be long enough for general community assessments (Fuller and Langslow, 1984). The additional slow walk circulating the site (see also Hartel et al., 2014) was made to reduce the negative impact of the short sampling period on the detection probability of inconspicuous species (cf. Scott and Ramsey, 1981; Fuller and Langslow, 1984).

Within 21 out of the 64 wooded pastures, bat communities were surveyed using SM3 bat detectors (Wildlife Acoustics, Inc.) placed at 1.5–2.0 m height at the centre of the site (Figure 4.3). Each site was surveyed once, between 8 June and 7 August 2015. Bat calls were identified semi-manually using Sonobat software (Szewczak, 2015) and the iBatsID system (Walters et al., 2012). Data used in this thesis only consider bat calls from 30 min after sunset until 30 min before sunrise to avoid recording commuting behaviour to and from foraging sites (see also Frey-Ehrenbold et al., 2013; Kalda et al., 2015).

Seed sowing experiment (Paper III)

For the seed sowing experiment, I selected four out of the 64 wooded pastures based on their similarity in terms of soil conditions and tree density. In each site, three mature Q. robur and three mature B. pendula trees were selected. Beneath the canopy of each tree, I established a permanent 0.5×0.5 m plot, coupled to an identical permanent plot outside the canopy. In each plot, 25 seeds (bought from Pratensis AB; www.pratensis.se) of eight selected grassland species were sown in 0.1×0.1 m randomly assigned sub-plots (and an additional sub-plot used as control). The species selected for the experiment represented four groups divided by seed mass and shade tolerance (two species in each category) (Figure 4.4). Prior to sowing, the ground was lightly scratched to simulate semi-natural conditions created by livestock. I counted the number of germinated seedlings four times the following year (2015).
4.3 Analysis

4.3.1 Measures of biodiversity

**Taxonomic diversity**

In Paper II, vascular plant diversity was estimated as *alpha* diversity (mean number of species per plot), *gamma* diversity (total number of species found within plots in a pasture) and *beta* diversity (*gamma/alpha* diversity; Tuomisto, 2010) (Figure 4.3). The diversity metrics were estimated both for all species and for grassland specialist species (see below). In Paper III, presence/absence data of each species in each plot was used to analyse species-specific responses to canopy cover at plot scale. In Paper IV, species richness of plants was derived from the *gamma* diversity metric. Bird and bat species richness were estimated as the total number of species found within a site during the study period (five visits for birds, one sample night for bats).

**Grouping of species**

Concerning plant communities in grasslands, specialist grassland species and generalist species may show divergent responses to differences or changes in the environment (Dupré and Ehrlén, 2002; Reitalu et al., 2012). Therefore, I defined grassland specialists, i.e. typical species of semi-natural grasslands which populations show substantial sensitivity to abandonment and/or fertilisation, based on Gustavsson et al. (2007) with some modifications (Paper II). In Paper III, grassland species were used for the seed sowing experiment, but the selection of species was constrained by requirements regarding shade tolerance and seed mass as well as availability from the seed provider (Pratensis AB). I made no species grouping for bird and bat communities within the scope of this thesis, as...
Wooded or treeless pastures?

Figure 4.4. Seed sowing experiment design. A: For each targeted tree individual, two experimental 0.25 m² plots were placed, one beneath the canopy (north side) and the other outside the canopy. Within each plot, 25 seeds of each of the selected grassland species were sown in a 0.01 m² sub-plot, in lightly scratched soil (the central sub-plot was used as control). B: Species selection for the seed sowing experiment, two species in each category based on shade tolerance (columns) and seed mass (rows). Modified from Paper III.

the focus of Paper IV was on general taxonomic and functional diversity patterns across environmental gradients.

Functional diversity

Paper IV looked into how functional diversity of plants, bats and birds varied along the environmental gradients considered. I used four functional diversity metrics: functional richness, functional evenness, functional divergence and Rao’s Quadratic entropy. The metrics cover a variety of measures of the functional space of biotic communities with different ecological meanings (Villéger et al., 2008; Mouillot et al., 2013). The functional space is the multi-dimensional space determined by species abundances (or presence) and their traits (Schleuter et al., 2010). The incidence-based volume of this functional space is typically called the functional richness. Taking into account abundance (i.e. abundance weighted calculations), functional evenness estimates how evenly distributed traits are within the functional space, whereas functional divergence estimates how distant the dominant species are from the weighted mean centre of the functional space. Rao’s Quadratic entropy measures the mean distance between pairs of species within the functional space, also weighted by abundance (Villéger et al., 2008; Mouillot et al., 2013).

To calculate functional diversity, any set of traits can be used, but it should reflect the variation in trait diversity that the specific study aims to target, as it has a major impact on outcomes and interpretation (Petchey and Gaston, 2006). In this thesis, I calculated functional diversity metrics using carefully selected traits coupled to six relevant trait groups available for all inventoried taxa: morphology, dispersal, foraging level, feeding resources, reproduction and life history (Table 4.2). Trait groups were used to balance the functional diversity metrics through weighted calculations and to facilitate interpretation of the results.

Functional diversity metrics were estimated using species’ relative frequencies within sites in combination with species’ traits: plant species frequencies (0-10) within the ten sample plots, bird species frequencies (0-5) across the five visits and bat species frequencies as the square root of the number of bat passes for each species within a site. Traits were accessed from available databases (Kleyer et al., 2008; Jones et al., 2009; Wilman
Table 4.2. Traits selected for the analysis. Traits were selected to represent six trait groups (left column). Numbers in brackets indicate number of levels for categorical traits (e.g. ‘dispersal mode (6)’ means that there were six different types of dispersal mode), letters in brackets represent Ellenberg indicator values (L = light; R = reaction of soil (pH); N = nitrogen; F = moisture).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Trait groups</th>
<th>Phenotypic traits</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>morphology</strong></td>
<td>seed mass</td>
<td>body mass</td>
</tr>
<tr>
<td><strong>dispersal</strong></td>
<td>dispersal mode (6)</td>
<td>wing length</td>
</tr>
<tr>
<td><strong>foraging level</strong></td>
<td>canopy height</td>
<td>foraging level (5)</td>
</tr>
<tr>
<td><strong>feeding</strong></td>
<td>Ellenberg (L, R, N, F)</td>
<td>food composition (8)</td>
</tr>
<tr>
<td><strong>reproduction</strong></td>
<td>seed number</td>
<td>clutch size</td>
</tr>
<tr>
<td><strong>life history</strong></td>
<td>life history (3)</td>
<td>longevity</td>
</tr>
</tbody>
</table>

et al., 2014; Myhrvold et al., 2015) and literature (Cramp et al., 1985-1994; Hill et al., 1999). Trait values were interpolated from other traits if necessary (van Buuren et al., 2015).

### 4.3.2 Statistical analysis

Several different analytical approaches were used within the scope of this thesis. Statistical methods are given in Table 4.3, whereas the text briefly summarises the analyses. All analyses were conducted using the computing environment R (R Core Team, 2017), using packages ade4 (Dray and Dufour, 2007), FD (Laliberté et al., 2015), glmmADMB (Fournier et al., 2012; Skaug et al., 2014), indicspecies (De Cáceres and Legendre, 2009), mgcv (Wood, 2011), mice (van Buuren et al., 2015) and vegan (Oksanen et al., 2017).

Table 4.3. Methods used in the papers of this thesis. For each paper, response and explanatory variables are given and the main statistical methods used. TrD = tree density, ShD = shrub density, TrDiv = tree diversity, TrSp = tree species composition, ForCov = proximate forest cover. GL(M)M = generalized linear (mixed) models, GAM = generalised additive models, RDA = redundancy analysis.

<table>
<thead>
<tr>
<th>Paper</th>
<th>Response data</th>
<th>Explanatory data</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Interviewed farmers</td>
<td>CAP, subsidies, motivation</td>
<td>-</td>
</tr>
<tr>
<td>II</td>
<td>Plant community: alpha, beta and gamma diversity and species composition</td>
<td>TrD, ShD, TrDiv, Compl., TrSp, ForCov, and soil pH, organic content, C:N-ratio</td>
<td>GLM, GAM, RDA, bootstrap</td>
</tr>
<tr>
<td>III</td>
<td>a) Germination success (eight species)</td>
<td>canopy presence (p/a), tree species (2)</td>
<td>GLMM</td>
</tr>
<tr>
<td></td>
<td>b) Plant community: p/a within plots</td>
<td>canopy cover, proportion of oak trees</td>
<td>GLMM</td>
</tr>
<tr>
<td>IV</td>
<td>Plant, bat and bird taxonomic and functional diversity</td>
<td>TrD, ShD, Compl., ForCov</td>
<td>GLM, 4th corner</td>
</tr>
</tbody>
</table>

**Farmers’ perspective on CAP, trees and biodiversity (Paper I)**

The interview data were not quantitatively analysed but qualitatively assessed and discussed. Hence, no direct analytical comparison between the interview data and the biological data was conducted. However, as a starting point and link between the different
parts of the thesis, the interview responses were put into context by comparing them with pasture structure in terms of trees, tree sizes and tree species.

**The effects of trees on understory plant communities (Paper II)**

I analysed plant species richness at plot (alpha diversity) and pasture (gamma diversity) scale as well as species turnover (beta diversity) in relation to the local environmental variables using linear (GLM; with and without quadratic terms) and non-linear models (GAM). To analyse plant species composition I used ordination methods calculating the relationship between plant species’ frequencies and environmental variables within sites. To estimate the potential contribution to plant species richness of the three tree density categories of the pastures (0-50, 50-100 or >100 trees/ha), I used a permuted bootstrapping method (permutation of the species communities from five randomised pastures within each of the three tree density categories). In Paper II, I investigated the effects of local environmental variables only, not considering the potential effects of surrounding landscape structure.

**Plant species-specific responses to tree canopies (Paper III)**

I compared the germination response of the eight studied grassland species between plots beneath and outside tree canopy, between the two tree species and how these effects potentially interact, using generalised non-linear mixed models (GLMM). These results were qualitatively compared to how species in the overall community assessment were affected by canopy cover and tree species dominance (regarding the two tree species selected for the experiment), which were analysed using binomial GLMMs. For these analyses, I split plant species into four categories based on seed mass and light dependency (i.e. light dependent vs. shade tolerant large seeded species and light dependent vs. shade tolerant small seeded species).

**The effects of trees on multi-taxa functional diversity (Paper IV)**

I analysed the response of functional (and taxonomic) diversity to tree density, shrub density, structural complexity and proximate forest cover using linear models (GLM; with and without quadratic terms). To better understand these responses, the effect of excluding one trait group at a time from the functional diversity metrics on their responses to the environmental variables was tested. In addition, I used a fourth corner analysis (Dray and Legendre, 2008) to analyse trait-specific responses to the environment. In this analysis, three matrices are used (species frequencies and environmental variables within sites together with species’ trait attributes) in order to estimate the correlation between traits and environmental variables.
5 Results and Discussion

5.1 Key findings

The results of this thesis are synthesised in the following sections. To provide an overview, six key findings are highlighted below, in relation to the three objectives they arose from:

A) Improve the understanding of farmers’ view on the CAP tree density limitation and how farmers potentially adapt to this regulation (Section 5.2)

- Farmers’ view on the CAP tree density regulation was neither completely negative nor positive, but as monetary subsidies from the EU are important for the farmers, the regulation definitely affected many farmers economically, but not necessarily how they managed trees in pastures (Paper I)
- Managing trees was considered an important part of pasture management also without the regulation and farmers showed strong appreciation for the beauty of both trees and landscape openness, as well as extensive knowledge about the values of trees in a social-ecological context (Paper I)

B) Investigate how taxonomic and functional biodiversity are affected by tree density along a complete tree density gradient in managed wooded pastures with long management continuity (Section 5.3)

- Trees had exclusively positive effects on taxonomic diversity of plants, birds and bats, with substantial increases along the entire tree density gradient up to more than 200 trees/ha, except for a slight drop concerning bird species richness at around 100 trees/ha (Paper II and IV)
- Functional diversity metrics across the three taxa showed little congruence, where bird and bat functional diversity responded mainly to other structural attributes of the wooded pastures and the proximate landscape, highlighting the need to consider multiple predictors of biodiversity across multiple taxa to understand how biodiversity is affected by management (Paper IV)

C) Increase the mechanistic understanding of biodiversity responses of multiple taxa in relation to trees in wooded pastures (Section 5.4)

- Tree species had a major impact on both species composition and germination success of grassland plant communities and the results suggest that there are different critical stages of how trees affect plant communities, depending on tree species and field layer community species (Paper II and III)
- Increased vegetation complexity within wooded pastures (mediated by trees, shrubs and structural complexity) affected mainly foraging/resource-use related traits among plants and birds, whereas the functional response of bat communities seem to be more related to their movements through and around vegetation at several spatial scales (Paper IV)
5.2 Farmers’ perspective (Objective A)

General perceptions about the tree density regulation

The overall effect of the tree density limit was neither good or bad according to the interviewed farmers, but resulted in a strong management and subsidy focus on trees and tree density. Having trees in pastures were considered a standard pasture management practice and thus the focus on trees in the CAP was not considered strange from the farmers’ perspective (Paper I). Nevertheless, subsidies make up for a substantial part of the farm income in the EU, ranging from 30 to 50% depending on country/region (Roellig et al., 2016; European Commission, 2017a). Therefore, regulations related to tree management have impact on the farmers, and some specific concerns were raised in Paper I regarding the tree density regulation. Most of them relate to the constant changes and shifts between different management guidelines within the CAP in general, where the tree density limitation forms a striking example. In general, the swift changes in regulations have caused mutual constraints regarding the trust and relationship between farmers and officials (e.g. at County Boards and the Board of Agriculture) (Paper I). Importantly, farmers highlighted the lack of harmony between the CAP and biophysical cycles, which relate to productivity but also to biodiversity values of the pastures. This lack of harmony was well exemplified by one of the responses from the farmers: ‘I thought that trees were good for the environment?’ (Paper I). Nevertheless, the interviewed farmers considered the communication between officials and farmers being better now compared to the beginning of the EU era.

Some of the farmers also discussed wider perspectives, in which the power of consumers and the market was highlighted as well as the debate regarding meat consumption, climate and biodiversity (Paper I). Wooded pastures easily become targets for the negative effects of meat production on greenhouse gas emissions (Garnett, 2009). In light of the climate impact of agricultural practices and meat production (e.g. Röös et al., 2013; Hedenus et al., 2014; Erb et al., 2017), a black and white view of land use impact arises, within which the social-ecological values originating from low intensity management of semi-natural grasslands are rarely considered. In Paper I, complaints about the market not promoting (Swedish) semi-natural pasture produced meat were also raised. However, wooded pastures exemplify an arena where nature conservation, production interests and possibly also reduced climate impact can meet (Olsson, 2012; Röös et al., 2013), which some farmers mentioned as a potential development for their farm (Paper I).

Views on tree management in wooded pastures

As the tree density regulation was introduced in 2008 (in Sweden), many farmers cut giant and dead trees with a following decrease in structural variation within pastures (Blom, 2010). Interestingly, the interviewed farmers would in general prefer to exclude an area with high tree density from the subsidy application rather than cutting down the trees, similar to findings of Raatikainen and Barron (2017), who found weak management adaptations to agri-environmental schemes among farmers in Finland. This reasoning related to the intrinsic values of the trees, especially the aesthetic values linked to traditionally managed agricultural landscapes in the region. These results are in line with the findings of Hartel et al. (2017), who also found a strong appreciation among farmers for the beauty and cultural identity of old oak trees in wood pastures in Romania, as well as with the attractiveness of trees among farmers in Australia (Seabrook et al., 2008). However, it is important to keep in mind that all the interviewed farmers had pastures defined having
Wooded or treeless pastures?

high nature or cultural values (defined by the County Administrative Board), which has given them greater freedom to keep trees in the pastures (Beaufoy et al., 2011), but potentially also additional insights into the high nature values of those lands. Hence, farmers in the study area may be exceptionally dedicated to values beyond the monetary input from the EU. Many of the interviewed farmers also have off-farm income, thus having more freedom to engage in management activities not necessarily leading to direct financial benefits. Several farmers mentioned the importance of keeping some kind of openness on the farm to maintain a visually appealing space between trees. Interestingly, openness has also been found to be a key motivation among farmers in Finland for maintained management of traditional rural biotopes (Raatikainen and Barron, 2017). Many farmers also mentioned the appreciation from other people: officials, researchers, visitors and neighbours (see also Burton (2004)). One farmer even stated that keeping the pastures and the landscape in a good condition comes first, before monetary returns, which exemplifies the farmers’ own appreciation of pasture management.

Similar to Hartel et al. (2017), the farmers in this area mentioned a wide range of benefits of trees, e.g. shelter and shade for animals, fruit picking and water retention, which show a high knowledge about pasture trees (see also Seabrook et al., 2008). In addition, the ecological values of pastures trees formed a common ground between farmers and officials for setting management goals. For instance, *Q. robur* and trees with visually appealing flowers are suggested as priority species among both groups. The preference for *Q. robur* among farmers is slightly contradictory though, as *Quercus* species have been found to inhibit grass and forb growth (cf. López-Carrasco et al., 2015), although beneficial for productivity during drought conditions (Frost and McDougald, 1989). The farmers also saved *Q. robur* trees inside the forest (if managing forest), probably for the impressiveness of large trees (aesthetics) or the biological values linked to old-growth trees (Bergmeier et al., 2010). Other tree species preferred were the flowering species *S. aucuparia* and *S. intermedia* (see also Figure 5.1), which could be considered an example of ‘charismatic’ species appreciated by the public (cf. Mikkelsen and Cracraft, 2001; McGinlay et al., 2017). The examples of saving the more rare species, or ‘odd’ species, relate to the unique environment that wooded pastures are. These tree species are otherwise rather rare in the region, and keeping them in pastures will contribute to an additional landscape feature with unique biodiversity values (cf. Hartel et al., 2014; Wood et al., 2017). Indeed, the relative proportion of large trees (>50 cm DBH) among the ‘odd’ species, e.g. *P. abies, Pinus sylvestris* and *Tilia cordata*, was relative high (>10%) in the studied pastures (Figure 5.1). The species-specific selection of which trees to keep (see also Harvey et al., 2011 and Barton et al., 2016), and the link between the view on trees of farmers, ecologists and policy implementers suggests a rather strong ecological basis for discussions on tree management and subsidies, encouraging the use of trees as starting points for discussing future sustainable management of wooded pastures. However, it also shows that a tree density regulation may be the wrong way to go, and just another example of simplification of nature (Scott, 1998), which may have negative consequences for biodiversity.

5.3 Biodiversity patterns in relation to trees (Objective B)

This thesis investigated plant community patterns in relation to tree density and other structural attributes within 64 wooded pastures, ranging from 3 to 214 trees/ha (corresponding to 6-77% canopy cover) (Paper II). Furthermore, taxonomic and functional diversity of plants, birds and bats were investigated in relation to tree density and other
variables within 21 wooded pastures, where tree density ranged from 12 to 214 trees/ha (Paper IV). The two most common tree species within the study sites were *Q. robur* and *B. pendula* (Figure 5.1), which also made up the clearest division in tree species composition by a gradient from *Q. robur* to *B. pendula* dominated pastures (Paper II) and they were therefore also used as target tree species in the seed sowing experiment (Paper III).

### 5.3.1 Taxonomic diversity

Species richness estimates across the three taxa studied in this thesis were not correlated (Paper IV). Therefore, the results are discussed mainly per taxon, including results from Paper II and IV. Interestingly, however, is that tree density had exclusively positive effects on plant, bird and bat species richness, despite the lack of congruence between the taxa (Figure 5.2; Paper IV), which is further discussed below.
Plants

The only vegetation structure variable that affected total species richness of plants (\textit{gamma} diversity) was tree density (Paper II and IV). Similar to Dorrough et al. (2006), \textit{gamma} diversity increased linearly by about 50\% along the tree density gradient (Figure 5.2), primarily driven by a substantial species turnover between plots within sites (\textit{beta} diversity) (Paper II). In contrast, the mean number of species per plot (\textit{alpha} diversity) was not significantly affected by tree density, but tended to decrease at 80–100 trees/ha. These tree densities correspond to 47–53\% canopy cover and is thus in line with earlier studies on small scale plant diversity in relation to trees in grasslands (e.g. Aavik et al., 2008 and Peterson and Reich, 2008), with parallel positive impacts on plant diversity beyond the plot scale due to the habitat patchiness created by trees (Tilman, 1980; see also Caruso et al., 2015). The findings in this thesis correspond to studies in both Australian wooded pastures and Estonian wooded meadows (Dorrough et al., 2006; Aavik et al., 2008), and further strengthen the view of trees as positive drivers of grassland plant diversity.

Grassland specialist species were affected by neither tree density nor any other structural variable (Paper II). Hence, grassland specialists within the studied wooded pasture are likely to be more dependent on management continuity than light availability (cf. Aavik et al., 2008; Reitalu et al., 2012; Caruso et al., 2015). However, the pastures’ patchiness probably contributes to areas of openings in the canopy cover that give space also for more light dependent species (Tilman, 1980). This was further confirmed by the bootstrap analysis, which showed that pastures with more than 100 trees/ha support the largest proportion of species (on average 77.3\%) and also the highest proportion of unique species (on average 11.6\%, Figure 5.3). Other structural attributes of the wooded pastures had no effect on plant species richness (Paper II).

Birds

Species richness of birds was strongly linked to vegetation characteristics in the wooded pastures. Species richness peaked at 100 trees/ha, with almost double as many species compared to the most open pastures (Figure 5.2). The positive, but saturating, effect of trees was expected (cf. Tellería, 2001; Laiolo et al., 2004; Catarino et al., 2016), and shows that the contribution of trees to biodiversity may not be as disproportionate as suggested (Fischer et al., 2010). Instead, the multiple values of trees in terms of nesting habitats and foraging space (Manning et al., 2006) seem to increase up to rather high tree densities (see also Jakobsson and Lindborg, 2017). Similarly, bird species richness peaked at 70 shrubs/ha (Paper IV). Shrubs may increase pasture complexity, improving the habitat quality for birds (Camprodon and Brotons, 2006) and by that positively affecting pasture bird communities (see also Söderström et al., 2001; Hartel et al., 2014).
The importance of habitat complexity for birds was further highlighted by the additional positive impact of structural complexity on species richness (Paper IV). Hence, in contrast to forest habitats (Charbonnier et al., 2016b), the complexity seems to be more important for bird species richness in semi-open habitats such as wooded pastures (see also Hovick et al., 2014). These local habitat characteristics have also been shown to strongly affect abundance and species composition of birds (Hovick et al., 2014; Myers et al., 2015; Jakobsson and Lindborg, 2017), which confirms that vegetation features are major drivers of bird communities in wooded pastures (Hartel et al., 2014). Shrubs also form traditional features of wooded pasture management (Vera, 2000; Bergmeier et al., 2010) and are important for tree regeneration (Bakker et al., 2004), but their presence in pasture environments are threatened because they tend to appear under too low grazing pressure or abandonment (Jones, 2008; Beaufoy et al., 2015).

**Bats**

Concerning bats, tree density was the only significant predictor of species richness (Paper IV), with almost doubled species richness estimates along the tree density gradient (Figure 5.2). Bat activity is predicted to increase with more (deciduous) tree cover (Kalda et al., 2015; Charbonnier et al., 2016a), thus the number of species was expected to increase (see also Lentinii et al., 2012). As bat activity and species richness have previously been shown to depend on insect abundance around trees (Le Roux et al., 2018), the results in Paper IV suggest that increasing tree densities contribute linearly to increasing food resources (cf. Müller et al., 2012).

The results are in contrast to Lumsden and Bennett (2005) and Fischer et al. (2010) who found optimum tree densities to be around 30 trees/ha in Australian wooded grasslands. Lumsden and Bennett (2005) suggest that this optimum relates to historical tree cover, thus the long tradition of forest grazing in Sweden may have made bats adapting to landscapes with dense tree cover, explaining the positive relationship between species richness and tree density (Figure 5.2). Importantly, the wooded pastures of today are among the few habitats dominated by deciduous trees in a landscape context where managed forests are considered being of rather poor habitat quality for bats (Wood et al., 2017). Wooded pastures are therefore key habitats for species linked to deciduous trees. Although the explanatory power of tree density on bat species richness was rather low (Paper IV) and landscape scale variables may override local habitat variables (Cisneros et al., 2015; Charbonnier et al., 2016a), local tree density also seems to be important by providing valuable foraging and roosting features for bats (Müller et al., 2012; Wood et al., 2017; Le Roux et al., 2018).

**5.3.2 Functional diversity**

Both plant and bat communities showed clear functional responses to the environment, but bird communities responded mainly in terms of species richness (Paper IV). Whereas increases in tree density explained most of the variation in taxonomic diversity across all taxa, similar effects on functional diversity were only found for plants. Instead, other vegetation attributes seem to be more important for the functional diversity metrics, especially regarding bats (Figure 5.4). In addition, there was little congruence between the three taxa. Plant and bat functional richness were the only corresponding metrics that correlated, despite the non-significant relationship between species richness of bats and plants (Paper IV; see also Aubin et al., 2013 and Eglington et al., 2015 regarding metric
dependent correlations between different taxa). This relationship was expected as arthropods are the predominant feeding resource for bats in this region and arthropod diversity is positively related to plant functional richness (Perner et al., 2005). In contrast to the bat communities, the bird species pool spans a wider feeding resource gradient, including seed- and fruit-eating species.

**Plants**

Tree density was the main predictor for plant functional diversity, in terms of functional richness and Rao’s Quadratic entropy (Paper IV). As these functional metrics are closely related to species richness (Schleuter et al., 2010; Mouillot et al., 2013), the responses to the environment logically followed the response of species richness (Figure 5.4). In contrast to Rolo et al. (2016), there was no decoupling of species richness and functional diversity along the tree density gradient. Hence, as tree density increases, functionally different species are added to the plant community without substantially affecting species present in pastures with low tree density (Paper IV). The lack of negative effects of trees on grassland specialists supports these results (Paper II). Increased pasture structural complexity also had a positive impact on Rao’s Quadratic entropy (Figure 5.4). This has previously been shown for landscape scale complexity (Ma and Herzon, 2014), meaning that complexity at multiple scales is important to sustain functionally diverse plant communities.

**Birds**

There were weak functional responses of the bird communities (Figure 5.4), despite expected guild specific effects, e.g. on open and forest specialist species (e.g. Catarino et al., 2016; Jakobsson and Lindborg, 2017). There were no significant effects of the explanatory variables on any functional diversity metric, but bird functional richness tended to decrease with increasing proximate forest cover (Paper IV). As forest cover in the surroundings increases, open habitat specialist species might disappear (cf. Jakobsson and Lindborg, 2017) and with that the functional space decreases. This contrasts the effects of shrubs, which were in general positive for bird functional richness up to intermediate densities, most likely driven by the positive effects of shrubs on many different species (Pärt and Söderström, 1999b; Söderström et al., 2001). Bird functional evenness was the only biodiversity metric that showed a tendency to respond negatively to tree density (Paper IV). Thus, the additional species along the tree density gradient are functionally dissimilar to the species occurring along the entire gradient, leading to decreased functional redundancy (Luck et al., 2013).

**Bats**

Concerning bats, their functional response to the environmental variables was much stronger compared to the response of species richness. The effects were rather complex, with different environmental predictors being most important for different diversity indices (Figure 5.4). Both tree density and proximate forest cover had a positive impact on functional richness (Paper IV). Hence, the functional space increases as tree cover increases at several scales (see also García-Morales et al., 2016) since additional species along both these gradients contribute to more functions within the bat community. How-
Figure 5.4. Main changes of taxonomic and functional diversity per taxon in relation to increases in the four environmental variables: shrub density (shrubs), tree density (trees), proximate forest cover (forest; represented by the green frame colour) and structural complexity (complex). Changes are described as linearly positive (+), linearly negative (-) or non-linear polynomial changes (e.g. ⌢), including marginally non-significant effects (n.s.; 0.05<p<0.06). Each box represents the functional space within a wooded pasture, a unique silhouette represents a “species”, and the size of the silhouette represents the abundance of that species. Taxon specific increases (decreases the opposite change) are symbolised as: species richness = more silhouettes; functional richness (FRic) = larger area covered by silhouettes; functional divergence (FDiv) = larger distance between large silhouettes (abundant); functional evenness (FEve) = more equal sizes of silhouettes and Rao’s Quadratic Entropy (Rao’s Q) = area covered by silhouettes and increased abundances of some species. Silhouettes from Freepik (www.freepik.com) and Vecteezy (www.vecteezy.com). The figure is based on results from Paper IV.

However, bat Rao’s Quadratic entropy showed a humpback response to proximate forest cover, peaking at around 35%, which shows that accounting for relative abundance of species results in a non-linear response to forest cover (Paper IV). Vegetation structures have previously been shown to be important for bats in semi-open environments (Adams et al., 2009). Indeed, the results in Paper IV show a complex that vegetation complexity increases functional redundancy (Luck et al., 2013) and that shrub density determines how functionally distant the dominant species within the bat community are (Figure 5.4). The effects of shrubs on bats may be guild-specific (e.g. Kalda et al., 2015), but it has also been suggested that more detailed estimations of understory vegetation might be required to properly investigate its effects on bat communities (Wood et al., 2017).
5.4 Underlying mechanisms of biodiversity patterns
(Objective C)

5.4.1 How trees affect plant species composition

In Paper II, trees had expected effects on plant community composition, through tree density and tree species composition (cf. Söderström et al., 2001; Aavik et al., 2008). The main shift along the tree density gradient was from light dependent to more shade tolerant plant communities. The effect of tree species composition suggests that tree management favouring specific tree species will have distinct effects on plant communities (see Paper I).

To increase the understanding of plant community patterns in wooded pastures, a seed sowing experiment was conducted in Paper III. In contrast to the predicted negative effects of canopy shading on germination (Ten Brink et al., 2013), the experiment revealed that large seeded shade tolerant species (as mature plants) germinated even better beneath tree canopies than outside. These results suggest that large seeded shade tolerant species benefit from a canopy induced germination, resulting in a competitive advantage that persists as the plant individual establishes. As expected (Thomaes et al., 2011), there were strong tree species specific effects on germination, resulting in significant interactions between tree species and canopy presence explaining germination success (Figure 5.5). Unfortunately, only one out of the four the small seeded species germinated (Paper III), most likely due to species variation in site condition requirements for germination (e.g. Whittington et al., 1988; Pérez-García et al., 2006). Hence, the expected germination advantage of large seeded species over small seeded species (Bruun and Ten Brink, 2008; Ten Brink et al., 2013) could not be thoroughly studied.

The link between germination and the mature plant community was weak (Figure 5.5), in line with Figueroa and Lusk (2001). Nevertheless, some species’ germination response did correspond to their occurrence in the community, which shows that species experience different critical stages during establishment. Whereas four out of the five sown species that germinated showed different responses to canopy presence depending on tree species (significant interaction), only 14% of the analysed species within the entire plant community showed tree species specific responses to canopy (Paper III). This suggests that the effect of specific tree species on grassland species may be erased as the plant community establishes, but the difference could also relate to the differences in measurements scales regarding the tree species. In the seed sowing experiment, individual trees of the two species were targeted (Paper III), whereas the community analysis was based on a rough species dominance variable (principal component axis 1; Paper II).

5.4.2 Drivers of functional diversity responses to the environment

One way to better understand functional responses of biotic communities to the environment is to look at how individual traits respond to the environment, which was done in Paper IV through a fourth corner analysis (Dray and Legendre, 2008). To further improve the mechanistic understanding of the functional diversity responses, a trait exclusion approach was implemented in Paper IV, excluding traits from one of the trait groups used (see Table 4.2). This novel approach helps to investigate functional diversity patterns and processes in depth. Overall, the functional responses of plants and birds were primarily affected by traits and trait groups linked to resource use and foraging, respectively.
contrast, bats’ functional responses were more dependent on traits related to manoeuvrability and other aspects of micro-habitat use (Table 5.1).

Plants

Resource competition is vital in plant community establishment (Belsky, 1994; Martens et al., 2000). It was therefore rather expected that increasing tree densities were associated with taller and more shade and nutrient tolerant species (Paper IV), in line with the results on species composition in Paper II. In addition, proximate forest cover had clear effects on plant traits. The unexpected relationship between light dependency and forest cover (Paper IV) could be related to land use history (Díaz et al., 1999), which was not included in the analyses. However, other trait responses (Figure 5.1) indicate that proximate forest cover may isolate the plant communities in wooded pastures, resulting in plant communities with a large proportion of species with good dispersal abilities (cf. Ehrlén and Eriksson, 2000).

Paper IV showed that the plant traits responding to tree density also affected the response of functional diversity. Higher tree densities supported plant communities with higher
Rao’s Quadratic entropy when including canopy height, whereas functional richness increased if including shade and nutrient tolerance traits in the functional metrics (Figure 5.1). Increased functional diversity in relation to higher tree density likely relates to pasture patchiness at intermediate to high tree densities, leading to large variation in light transmission through canopies (Martens et al., 2000).

**Birds**

Local habitat variables have previously been shown to affect specific bird breeding/nesting traits (Hartel et al., 2014), but the focus of this thesis was habitat use in general rather than breeding conditions within the pastures. As tree density increased, seed eating ground foragers decreased, whereas mid-high foragers increased (Figure 5.1). Thus, the effect of local vegetation characteristics on bird foraging was confirmed (Fuller, 2012; Ikin et al., 2012), with tree density as the main predictor (Paper IV). In addition, less mobile species (with relatively shorter wings) were more common in pastures surrounded by more forest (Figure 5.1), most likely explained by forest dependent species being negatively affected by fragmentation (Amos et al., 2014).

The trait group exclusion analysis did not further explain the negative effect of tree density on bird functional evenness, as a variety of trait groups affected this relationship. The response of functional richness to shrub density and proximate forest was driven mainly by birds’ foraging levels (Figure 5.1). Decreased variation in foraging levels may be a result of a reduced number of open habitat species as proximate forest cover increases (Jakobsson and Lindborg, 2017). In contrast, the habitat heterogeneity created by shrubs (Bakker et al., 2004) facilitates co-existence of species with varying foraging levels up to a certain shrub density where ground foragers are negatively affected (Paper IV).

**Bats**

In contrast to plants and birds, bat traits did not show as clear responses to the environment, which might be explained by the small spatial scale used in this thesis (Cisneros et al., 2015). Nevertheless, increased variation in longevity and forearm length explained many of the functional responses to the environment, including the effect of tree density (Figure 5.1). Forearm length is a trait closely linked to a bats’ manoeuvrability (Hodgkinson et al., 2004) and has previously been shown to affect bats’ responses to vegetation structure (Jung et al., 2012). The results indicate that bats with shorter forearms are favoured by denser tree cover at multiple scales, while bats with longer forearms persist, which results in increased functional richness in relation to increased tree density and proximate forest cover (Paper IV). Open specialist species have in general longer forearms Müller et al. (2012) and prefer foraging above forest canopies (Russ, 2012), which may contribute to the increased functional richness.

Bat longevity also affected the increase in functional richness along the tree density gradient, as well as all other metrics’ responses to different environmental variables (Figure 5.1). Thus, there are complex patterns of bat functional diversity metrics, but the effect of longevity suggests that many patterns are related to the presence of specific bat guilds (Paper IV; see also Müller et al., 2012).
Table 5.1. Results from the trait based approach, with environmental variables as row names and trait groups (see text) as column names. In grey rows, the contribution of including a specific trait group to how each functional diversity metric respond to the environmental variables is described. If a metric is present in a grey cell, it means that the metric’s response to the corresponding environmental variable (left column) is affected by that trait group (column headings). Responses are described as linearly positive (+), linearly negative (-) or non-linear polynomial changes (e.g. ↗). FRic = functional richness, FEve = functional evenness, FDiv = functional divergence, Rao’s Q = Rao’s Quadratic entropy. In white rows, the effect of environmental variables (left column) on specific traits belonging to the trait groups (column headings) is given. Arrow pointing upwards means positive effect; arrow pointing downwards means negative effect; flat arrow means that a categorical trait was affected. Photos: Simon Jakobsson.

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6 Implications for policy, management and research

This thesis provides important findings concerning potential effects of the CAP tree density limitation on management and biodiversity of wooded pastures. The thesis questions the relevance of tree number regulations regarding pasture management but also provides findings that are valuable for further elaboration of the subsidy system. The fact that the EU in November 2017 announced to open up for excluding the tree density regulation from the CAP therefore seems promising (European Commission, 2017c). I hope that this work has contributed to these changes, as it has contributed to national level evaluations of the Swedish rural landscape programme (Smith et al., 2016). In addition, the results provide important insights into complex biodiversity patterns in wooded pastures and highlight several future directions for research.

6.1 Policy and management implications

- High tree densities increase biodiversity, but the variation between pastures contributes to large scale habitat heterogeneity which is essential for biodiversity

This thesis shows that tree density is the main positive predictor of species richness of plants, birds and bats (Paper II and IV). Hence, if high species richness across multiple taxa is desired, high tree density is positive for biodiversity. However, there is a substantial species turnover along the tree density gradient (Paper II, see also Jakobsson and Lindborg, 2017; Wood et al., 2017), and trees are not always positive for biodiversity. I therefore stress the value of between pasture variation, as pastures with different tree densities will capture different assets of biodiversity and increase landscape level heterogeneity.

- Continued grazing of wooded pastures is important to maintain habitat heterogeneity and high biodiversity values

The positive effects of tree density on biodiversity found within this thesis are results of continuous low-intensity grazing maintaining the high biodiversity values linked to habitat heterogeneity (Paper II and IV, see also Dufour et al., 2006 and Oldén et al., 2016). This is in contrast to the negative impacts of more trees as a result of abandonment (Öckinger et al., 2006; Oldén et al., 2016). Therefore, it is important to maintain the grazing management of wooded pastures, irrespective of their tree density. This may, in turn, counteract the negative impact of habitat and landscape homogenisation on biodiversity (Tews et al., 2004; Gámez-Virués et al., 2015).
• **Multiple taxa need to be considered when setting policy guidelines, otherwise important biodiversity values may be overlooked**

The results of Paper IV showed that there was little congruence between taxa across diversity metrics. The thesis thus confirms how responses of biological communities are sensitive to choice of taxon and diversity metric, which highlights the need to consider multiple organism groups in policy and management (see also Pärt and Söderström, 1999a). Plants, which are commonly used as biodiversity indicators for grasslands, do not cover the whole biological response of agro-forestry systems such as wooded pastures (e.g. Torralba et al., 2016). Plants may also be less good predictors of ecological functioning compared to other organism groups (Lefcheck et al., 2015). I argue that better acknowledgement of the values of multiple organism groups is one of the most important improvements needed in policy guidelines.

• **Taxonomic diversity is a more feasible tool for policy-makers and managers compared to functional diversity, due to its complex responses to the environment**

Paper IV showed that traits primarily linked to foraging and use of resources determined the functional responses of plants and birds, whereas the functional responses of bat communities were mainly driven by traits linked to habitat use. These rather complex responses of functional diversity make me question whether these are relevant metrics in a policy perspective (see also Jonason et al., 2017). I stress that more research (see section 6.2) is needed before implementing functionality aspects of biodiversity into guidelines for pasture management.

• **The flexibility in policy directives should be increased to acknowledge the multiple social and ecological values of wooded pastures**

A categorical tree density limitation in one end and farmers potentially not following that in the other end indicates some inefficiency in the policy system (Paper I). The social-ecological link that applies to wooded pasture habitats and management should encourage more flexibility in policy guidelines to acknowledge the multiple values of wooded pastures. In addition, tree density was a less important predictor for functional diversity, which was closer related to other attributes of the wooded pastures (Paper IV). From a policy perspective, I therefore suggest that the presence of multiple vegetation features should be considered in policy and management to ensure conservation of pastures’ functional values.

• **Trees as starting points in management strategies can be an effective way of steering pasture management, as long as farmers’ and researchers’ knowledge about the effect of trees on pasture productivity, biodiversity and functioning are considered**

Farmers value trees as key features in their pastures for livestock, biodiversity and landscape aesthetics (Paper I, see also Blicharska and Mikusiński, 2014 and Hartel et al., 2017). The selective management of different tree species highlighted in Paper I emphasises the key role of farmers structuring the wooded pastures (see also Harvey et al., 2011 and Barton et al., 2016). Further, trees have different effects on biodiversity depending on which tree species make up the pastures (Paper III). Exploring alternative pathways and tools (e.g. Barton et al., 2016) for guiding tree management in wooded pastures to support high biodiversity values is therefore an important task for the future. Based on this thesis, I suggest that trees, being easily estimated and tangible structures of the pastures, should form key features for communication between stakeholders.
6.2 Future directions for research

- *It is important to disentangle the relative contribution of wooded pastures to biodiversity at a landscape scale*

Although this thesis considered only the proximate forest cover to account for the surrounding landscape, there were indications of landscape effects on biodiversity patterns. However, the relative contribution of different landscape elements to the landscape scale biodiversity has been less studied. To properly target the effects of biodiversity on ecosystem functionality, effects across different scales need to be investigated (Pasari et al., 2013). For example, Wood et al. (2017) showed the substantial contribution of wooded pastures to bat diversity in comparison to open fields and forests. Hence, similar approaches would be of high value to further inform policy guidelines at landscape scale rather than at the habitat scale (see also Lindborg et al., 2008).

- *Research should target small-scale habitat features, such as shrubs, to understand their effects on biological communities*

The results show that micro-habitat attributes of wooded pasture, such as shrubs and vegetation complexity, are not only traditional attributes of wooded pastures but also very important predictors of biodiversity. However, shrub density and structural complexity may not be detailed enough measures to thoroughly understand the responses of biodiversity to small-scale habitat features (cf. Müller et al., 2012 and Wood et al., 2017). Novel scientific approaches to understand the effects of habitat complexity are therefore needed.

- *Studying the response of biodiversity in relation to tree micro-habitats and tree species will increase the understanding of biodiversity patterns in wooded pastures*

This thesis has focused on the density of trees, but several other aspects of trees affect biodiversity. Habitat use of especially bats and birds may depend on tree micro-habitats such as cavities, bark cracks and deadwood (Regnery et al., 2013). Trees may also contribute to important micro-habitats for plants, e.g. by providing shade and thereby increase plants’ resistance to drought (Frost and McDougald, 1989). The effects of different tree species on grassland plant communities (Paper II and III) may, together with tree size, have a major impact also on other assets of biodiversity (Barbier et al., 2008; Kiebacher et al., 2017; Le Roux et al., 2018). Targeted studies investigating the responses of biodiversity in relation to tree micro-habitats and tree species are therefore needed in order to increase our understanding of the complex biological responses to wooded pasture attributes.
7 Concluding remarks

This thesis has exemplified how the CAP tree density regulation has failed to capture multiple biological values of wooded pastures. Positive effects of trees were found for plant, bird and bat species richness, despite the lack of congruence between these species groups. Looking beyond species richness, only plant functional diversity partly followed the patterns of species richness, whereas bird and bat functional diversity were dependent on other vegetation features. In addition, clear species-specific effects of different tree species and a variety of trait-effects on functional diversity responses were found. The results suggest that multiple taxa, environmental variables and diversity metrics need to be considered in order to inform policy for biodiversity conservation. Since considering all these aspects is impractical and unrealistic, I suggest that multiple taxa is most important to consider because that will cover a wide range of biological values. In order to do so, however, values of multiple vegetation features need to be acknowledged. Concerning functional diversity, I do not think it can be handled in policies yet due to its complexity.

Based on the results from this thesis, I believe that trees nevertheless may form fairly good starting points when discussing pasture management among stakeholders. Trees relate to a range of social and ecological values in wooded pastures, and belong to regular management practices. I hope that the role of trees as major drivers of multiple social-ecological values will be better acknowledged in the future, in combination with appreciation of between pasture variation created by farmers’ different management strategies. If so, there are better chances to increase heterogeneity of the pastures and within agricultural landscapes as a whole, with subsequent positive effects on biodiversity.
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Wooled or treeless pastures?


Lee MB, Martin JA. 2017. Avian Species and Functional Diversity in Agricultural Landscapes: Does Landscape Hetero-
Wooded or treeless pastures?


