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Strategic landscape-level integration of biomass production and ecosystem services at European level

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Academic dissertation

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ABSTRACT

Biomass systems have been increasingly adopted across Europe as sources of renewable energy and bio-based products. Particularly, fast-growing plantations have expanded rapidly in response to the need to reduce carbon emissions, mitigate climate change and strengthen energy independence. Beyond their productive role, biomass systems can provide multiple environmental services to the landscapes where they are embedded. However, these benefits are highly context dependent. Additionally, spatial data on biomass systems remains scattered and decentralized, limiting the capacity to study their effects.
To address this gap, this thesis compiles spatial data on biomass systems across Europe, characterizing their surrounding land use context, and exploring spatial configurations through which these systems can enhance landscape properties and ecosystem services. Using available data on biomass system locations alongside land use datasets, we assessed land use diversity, modelled ecological connectivity, and applied multi-objective spatial planning to optimize management actions across trade-offs between profitability and ecosystem service provision.
Our results show that poplar and willow plantations hold the highest potential to diversify agricultural landscapes, owing to their relatively small stand sizes and predominant location within intensive agricultural matrices. In contrast, eucalypt plantations pose a risk of landscape homogenization, driven by their large stand sizes and occurrence within predominantly forested surroundings. At the river basin level, poplar plantations can work as steppingstones connecting large forest patches, but their effectiveness depends on their spatial configuration and the dispersal ability of the studied species. Spatial optimization of poplar plantation management revealed their potential role in sustaining ecosystem services under stringent conservation scenarios. Coupled with riparian forests, they can achieve both economic viability and desirable ecological outcomes in working landscapes.
Overall, this thesis makes a novel contribution to the understanding of biomass systems in Europe, providing a spatial framework to support land managers, policymakers, and researchers in designing landscapes that balance productivity with sustainability.

Keywords: fast-growing plantations, land use change, ecological connectivity, biodiversity, bioenergy, multifunctional landscapes

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Lleida, 9th June 2026

Sara Pineda-Zapata

LIST OF ORIGINAL ARTICLES

This thesis is based on data presented in the following articles, referred to by the Roman Numerals I-III.

I Pineda-Zapata, S. & Mola-Yudego, B. (2025). European Biomass Production Systems: Characterization and Potential Contribution to Land Use Diversity. GCB Bioenergy 17, no 7: e70057. https://doi.org/10.1111/gcbb.70057

II Pineda-Zapata, S., Morán-Ordoñez, A., Mola-Yudego, B., Duflot, R. (2026). Strategic placement of plantations enhances forest connectivity for birds in agricultural landscapes. Lands Ecol 41: 54. https://doi.org/10.1007/s10980-026-02316-z

III Pineda-Zapata, S., Hermoso, V., Coll, L., Dimitriou, I., Englund, O., Mola-Yudego, B., Salgado-Rojas, J. Multiple objectives, one landscape: spatial optimization balancing timber profit and ecosystem services provision in a mixed forest-plantation area. Manuscript

Sara Pineda-Zapata is responsible for the compilation of this thesis and is the first and corresponding author for all articles. Papers I and II are reprinted with kind permission from the concerned journals.

TABLE OF CONTENT

ABBREVIATIONS AND DEFINITIONS

Abbreviations

BAU	Business as Usual
CLC	Corine Land Cover
CAP	Common Agricultural Policy
ES	Ecosystem services
FGP	Fast Growing Plantations
LUDI	Land use diversity index
SRC	Short Rotation Coppice
SRP	Short Rotation Plantations
SOC	Soil organic carbon

Definitions

Biomass production systems: In this thesis, biomass production systems refer broadly to perennial lignocellulosic systems, including woody plantations and perennial grasses. Plantation systems refer specifically to woody plantations regardless of end use. The plantation categories used (SRC, SRP, FGP) reflect management orientation, rotation length, and productive objective rather than strict species boundaries. Poplar, for instance, may fall under SRC, SRP, or FGP depending on management. Not all fast-growing plantations are primarily destined for energy biomass, and a significant share can target veneer, pulp, or timber markets.

INTRODUCTION

Biomass systems relevance

Globally, the increasing demand for biomass and bio-based products increases the pressure on natural and managed ecosystems (Muscat et al. 2021). Within this global context, in Europe, biomass expansion is also driven by climate policy, with the European Union implementing ambitious measures such as the European Green Deal to achieve climate neutrality by 2050 (European Commission 2019). On top of ambitious decarbonization goals, energy security has also arisen as another pressing need in Europe, further accelerating interests in biomass production (Clifton-Brown et al. 2023).

To meet these goals and increasing demands, biomass systems have appeared as a promising strategy. These systems are key sources of bioenergy and biomaterials, displacing the need to rely on fossil fuels, thus advancing sustainable goals to reduce climate change impacts, and contributing actively to energy security (Ali et al. 2025).

Although terminology varies across literature, lignocellulosic biomass production systems can be broadly divided into woody plantations and perennial energy grasses, both constituting key feedstocks for second-generation bioenergy as well as a range of bio-based products and materials (Mola-Yudego et al. 2017). Among perennial energy grasses, the main species cultivated in Europe are *Miscanthus* spp. and reed canary grass (*Phalaris arundinacea*). Both are characterized by short annual harvest cycles and high biomass yields per hectare (Lewandowski et al. 2016; Mola-Yudego et al. 2021). Woody lignocellulosic plantations may encompass three main typologies that differ in species, management intensity, and rotation length. Short-rotation coppice (SRC) relies on the natural resprouting ability of species such as willow (*Salix spp.*) and poplar (*Populus spp.*), harvested every 2–5 years (Baker et al. 2022). Short-rotation plantations (SRP) are non-coppiced systems (e.g., *Eucalyptus spp*.), with rotations of 12-14 years (Ruiz et al. 2008), managed primarily for pulp and biomass (Tomé et al. 2021). Fast-growing plantations (FGP) are primarily oriented toward the production of higher-value wood products. This group includes species like radiata pine, but poplar species can also fall within this category. In Spain, for instance, poplar plantations are commonly used for veneer and wood panels, with rotation periods of around 12+ years (Rodríguez et al. 2010).

Because biomass systems are highly heterogeneous and encompass a wide range of forms and definitions, developing centralized and harmonized datasets is challenging. This lack of consistency limits further research on these systems as well as the ability of farmers and policymakers to support and advance their adoption (Lindegaard et al. 2016).

Impacts and trade-offs

Despite their potential as a renewable energy source, the sustainability of biomass systems remains highly debated (Mola-Yudego et al. 2024), and several studies have highlighted the negative effects they may have on ecosystem services. Biodiversity has been one of the most frequently cited concerns, with researchers arguing that the large-scale deployment of biomass systems would reduce species richness through land use change, particularly affecting open habitat species such as reptiles, butterflies, and birds (Louette et al. 2010). Large-scale plantations also threaten forest specialist species dependent on native and old-growth forests, with studies showing detrimental effects on species such as the Lesser Spotted Woodpecker when poplar plantations dominate the landscape (Porro et al. 2020). The impact on water budgets at the basin level has also been examined, with poplar plantations found to consume approximately 20% of aquifer recharge (Folch and Ferrer 2015). Furthermore, their carbon sequestration potential has also been questioned, as land use change may offset initial sequestration benefits (Searchinger et al. 2008).

However, an increasing body of literature has shown that these impacts depend on several variables and contexts. For instance, Berg. (2002) demonstrated the effects of adjacent habitats and plantation height on bird communities, with most species recorded in taller plantations, and positive effects observed when plantations were located within intensive farmland. In line with this finding, several studies have explored the benefits of incorporating perennial biomass systems into dominant agricultural matrices. This process, often referred to as perennialization, can enhance the provision of ecosystem services such as pollination, pest and flood control, water regulation, and climate change mitigation (Asbjornsen et al. 2014; Englund et al. 2020, 2023).

The relationship between biomass systems and riparian areas, particularly in poplar plantations, has also been studied, largely due to the species' preference for flooded areas due to its high water requirements. Martín-García et al. (2013) highlighted the effects of poplar plantations in Mediterranean riparian areas, emphasizing that although these plantations do not represent optimal habitats, they can support important forest bird communities. Likewise, Chiatante et al. (2019) showed the role of poplar plantations in northern Italy to connect isolated forest patches in fragmented landscapes. In fact, when located along river corridors that link large forest patches, poplar plantations have been found to increase potential functional connectivity for forest birds in Spain (Pineda-Zapata et al. 2026).

The potential multifunctionality of biomass production has also been explored, highlighting that location, spatial design, and sustainable management practices can aid in achieving multiple ecosystem services. Phytoremediation has been a popular option, particularly in Sweden, where willow plantations irrigated with wastewater as fertilizer can act as natural filters, helping to purify the water. Some *Salix* clones have also been shown to be highly efficient at removing heavy metals, such as cadmium, from arable soils (Berndes et al. 2008).

These examples demonstrate that the environmental effects of biomass systems are highly context-dependent, and that targeted management actions, combined with adequate spatial planning, can improve landscape sustainability and multifunctionality. Thus, understanding which specific actions yield the greatest ecological benefits is key to guiding sustainable biomass expansion.

The importance of management and spatial planning

At the field scale, Dauber et al., (2010) identified several biodiversity-friendly management practices, including the application of different harvesting cycles and the inclusion of different varieties to maintain diverse age structures and increase heterogeneity. Maintaining a certain amount of understory vegetation, and encouraging biological control instead of herbicides or pesticides are also recommended management measures to enhance biodiversity in SRC (Vanbeveren and Ceulemans 2019). Furthermore, longer rotation periods in poplar plantations have been shown to benefit understory forest plants (Archaux et al. 2010), while also improving soil biochemical properties (Pellegrino et al. 2011).

Other properties, such as soil organic carbon (SOC) levels, can be enhanced in poplar plantations through sustainable management practices. These include reduced tillage and the establishment of polycyclic systems, where poplars are grown alongside other tree species with different growth rates. Additionally, the application of manure and pruning residues as fertilizers is an underutilized practice that can contribute to a more sustainable cultivation system (Antoniella et al. 2024). There is also an important relationship between poplar genotypes and water availability. It has been studied how selecting genotypes that are adapted to specific climatic and hydrological conditions can promote a more efficient and sustainable use of water resources (Zalesny et al. 2019).

Although some management practices demonstrate the potential to enhance the sustainability of biomass systems, land and financial resources remain limited. Moreover, profitability is a key consideration for farmers when investing in plantations. Therefore, management efforts must be strategically targeted to account for these economic, logistical, and spatial constraints. Spatial prioritization approaches offer valuable tools to identify where these efforts can be most effectively applied. Such approaches have been widely used in conservation science to identify and prioritize areas for biodiversity (Hermoso et al. 2020; Morán-Ordóñez et al. 2025), and have more recently evolved to also determine what management actions are needed to meet conservation goals(Brown, 2015).

Selecting which management actions to implement and where to allocate them across a landscape is a complex task. Decision-support tools such as MARXAN with Zones (Watts et al. 2009), and Zonation (Lehtomäki and Moilanen 2013) have been widely used to address such challenges in conservation planning. More recently, the R package *prioriactions* (Salgado-Rojas et al. 2025) has applied exact mixed-integer programming approaches to optimize multiple management actions simultaneously. These tools have also been adapted to production landscapes (Pohjanmies et al. 2019) showing strong potential to guide plantation management by identifying strategies that enhance ecosystem service provision while maintaining economic profitability. Importantly, many of these approaches incorporate landscape connectivity, which is particularly relevant for biomass systems often embedded within highly fragmented agricultural landscapes (Önal et al. 2023).

Nevertheless, the implementation of sustainable strategies would ultimately depend on policy frameworks that can shape land-use decisions and incentivize adoption for farmers. At the EU level, the Common Agricultural Policy (CAP) has progressively incorporated environmental objectives, and the 2023–2027 reform introduced eco-schemes and agroforestry support mechanisms that offer renewed opportunities to align biomass production with biodiversity and connectivity goals (Regulation 2021/2115). However, authors have pointed to a lack of clarity surrounding the environmental benefits of short-rotation plantations (Lindegaard et al. 2016), and the contribution of current eco-schemes to climate and biodiversity objectives for SRC systems remains uncertain (Geier et al. 2025). Bridging the gap between the scientific understanding of biomass systems' ecological effects and the design of effective policy instruments, therefore, remains a pressing challenge.

Aims of this study

To achieve a more sustainable development of biomass plantations and build multifunctional landscapes that can meet global demands while sustaining natural ecosystems, understanding their site-specific effects and planning landscapes accordingly is essential. This thesis addresses these challenges through three studies conducted at different spatial scales:

Study I, at a European scale, aims to characterize biomass production systems and contribute to filling the lack of centralized spatial data that currently limits our understanding of the contexts in which plantations can be environmentally detrimental or beneficial.

Study II assesses, at the basin level, how poplar plantations may enhance functional connectivity in highly agricultural landscapes and support broader conservation frameworks such as the Natura 2000 network.

Study III, at a regional scale in Catalonia (NE Spain), examines the management of landscapes where poplar plantations and riparian forests coexist, applying a spatial optimization model to evaluate how different management actions can be allocated to maximize economic returns while maintaining the provision of key ecosystem services and connectivity.

MATERIALS AND METHODS

Study area

This thesis adopts a multi-scale approach to examine the role of biomass plantations across spatial contexts. The research progresses from a European-scale assessment of biomass systems (**Study I**) to a regional analysis conducted in two agricultural sub-basins in Spain and France (**Study II**), and finally to a local case study in the province of Girona, Spain (**Study III**).

For **Study I**, we created a database of biomass systems comprising seven species among Europe, in the countries of Austria, Belgium, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany (Lower Saxony, Brandenburg, and North Rhine-Westphalia), Italy (Toscana and Lombardia), Latvia, Netherlands, Portugal, Slovakia, Spain, Sweden, and the UK (England). These countries were mainly selected because of the presence of fast-growing species representing different biomass systems.

As we aimed to analyze the role of plantations in agricultural landscapes, based on the first study, we selected two sub-basins with predominant agricultural cover and the presence of poplar plantations (**Study II**). We focused on the Pisuerga and Oise rivers in Spain and France, respectively. Both regions are characterized by long-established commercial poplar plantations, traditionally managed for industrial wood production, particularly veneer and plywood (Oliveira et al. 2020; Rahayu et al. 2015).

The sub-catchment of the Pisuerga river is characterized by riparian forests with poplar and willow occurring naturally. Due to the high-water availability, hybrid poplar plantations are a common land use, as well as the cultivation of cereals. This sub-basin also includes several N2000 sites for the management and conservation of habitats of community interest, such as alluvial and gallery forests of *Fraxinus excelsior*, *Alnus glutinosa*, *Populus alba,* and *Salix alba* (MITECO). Similarly, in the Oise valley in France, poplar plantations are a long-established land use, forming part of the regional landscape and economy, and are closely associated with managed floodplains and riparian zones (Direction Départementale de l'Équipement de l'Oise 2008).

Finally, **Study III** was carried out in a smaller area located in the province of Girona, Spain. Girona has a promising poplar industry, being the only region in Spain exporting roundwood of this species (Crespo Pinillos and Souto Suárez). The area was also interesting for our study due to the presence of protected riparian elements such as the N2000 sites of Riberes del Baix Ter and Riu i Estanys de Tordera.

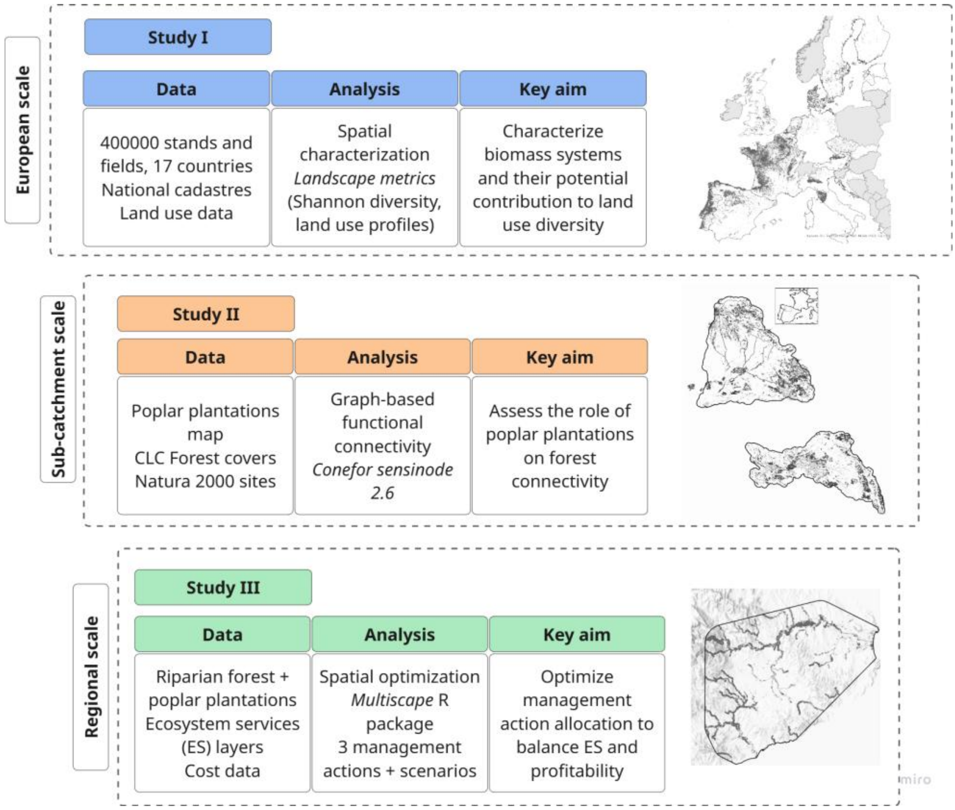

Figure 1. Methodological framework of the thesis, summarizing the data sources, analytical approaches, and study aims of each study. Maps illustrate the study areas for **Study I** (Europe), **Study II** (Pisuerga and Oise sub-catchments, Spain and France), and **Study III** (Girona, NE Spain).

Data sources

Biomass systems spatial data

Spatial information on biomass production systems, including fast-growing plantations and perennial grasses, was sourced from national cadaster records and country-specific land-use inventories. A complete list of consulted datasets by country is provided in the supplementary material of **Study I**.

For **Study II** and **Study III**, poplar plantation geometries were obtained from national mapping products: the Poplar Plantation Map (Ministerio para la Transición Ecológica y el Reto Demográfico 2020) for Spain, and the BD Forêt 2.0 dataset (IGN 2021) for France.

Land uses

To contextualize the role of plantations in the landscape, we integrated land cover data retrieved from the CORINE Land Cover 2018 vector layers (European Environment Agency 2019). This dataset was additionally used to extract forest patches and create a joint dataset of poplar plantations and forests that was used to model functional connectivity (**Study II**). Similarly, land uses for **Study III** were extracted from the CORINE Land Cover Riparian Areas 2018 dataset (European Environment Agency 2021b) to be used jointly with poplar plantations polygons as planning units.

In addition to land uses, in **Study II**, we aimed to understand the role of poplar plantations in contributing to the Natura 2000 network. The Natura 2000 comprises a network of sites established for the management and protection of habitats and species of community interest based on two different European directives (Habitats Directive 92/43/EEC- Birds Directive 2009/147/EC). The delimitation of these sites was obtained from the Natura 2000 EU database (European Environment Agency 2021a).

Ecosystem services and habitats distribution

To evaluate the provision of ecosystem services in **Study III**, we used the spatial dataset provided by Zurbaran Nucci et al., 2024, from which we selected three ecosystem services: flood control, carbon sequestration, and soil retention.

We also used the EUNIS habitat type probability maps (European Environment Agency 2023) to identify four riparian habitats listed in Annex I of the EU Habitats Directive (Council Directive 92/43/EEC) — the European Union's main legal framework for biodiversity conservation. These habitats are classified as habitats of community interest, requiring member states to implement conservation measures and designate Special Areas of Conservation.

Biomass system's characteristics and land use analysis

Characterization of biomass systems (**Study I**) was based on their location, size, and surrounding landscape. We created spatial buffers of 1 km for all polygons and extracted land cover information within. We used land cover as a proxy for land use and categorized it into three main group: forest, agricultural land, and others, to estimate a land use diversity index (Eq 1):

$$\boldsymbol{LUDI_k} = \sum_{i=1}^{m}(\boldsymbol{p_i ln p_i}) \qquad \text{(Eq 1)}$$

Where $\boldsymbol{p_i}$ is the proportion of land use class *I* inside the buffer for biomass production system *k*.

Landscape connectivity

Landscape connectivity can be broadly classified into two types: structural connectivity, which reflects the spatial configuration and availability of habitat patches, and functional connectivity, which incorporates organisms' characteristics such as dispersal ability and habitat suitability (Martínez-Richart et al. 2024). Following this classification, the connectivity analyses presented here estimate movement potential based on species traits and landscape structure, rather than empirically observed dispersal events. Specifically, functional connectivity (**Study II**) falls within methods that can operate with organism characteristic data sourced from the literature rather than field movement data, while structural connectivity (**Study III**) relies on landscape characteristics to model potential movement flow across the landscape, reflecting the permeability of the matrix to movement.

Functional connectivity was assessed in **Study II** to evaluate how poplar plantations contribute to movement potential for forest bird species within agricultural landscapes. Three bird species were selected based on their natal dispersal distances (Paradis et al. 1998): the common chaffinch (*Fringilla coelebs*, 0.79 km) as a limited disperser, the great spotted woodpecker (*Dendrocopos major*, 5.9 km) as an intermediate disperser, and the blackcap (*Sylvia atricapilla*, 17.5 km) as a long-distance disperser. Four scenarios were built by progressively adding habitat patches to evaluate the net contribution of plantations to forest connectivity (Figure 2).

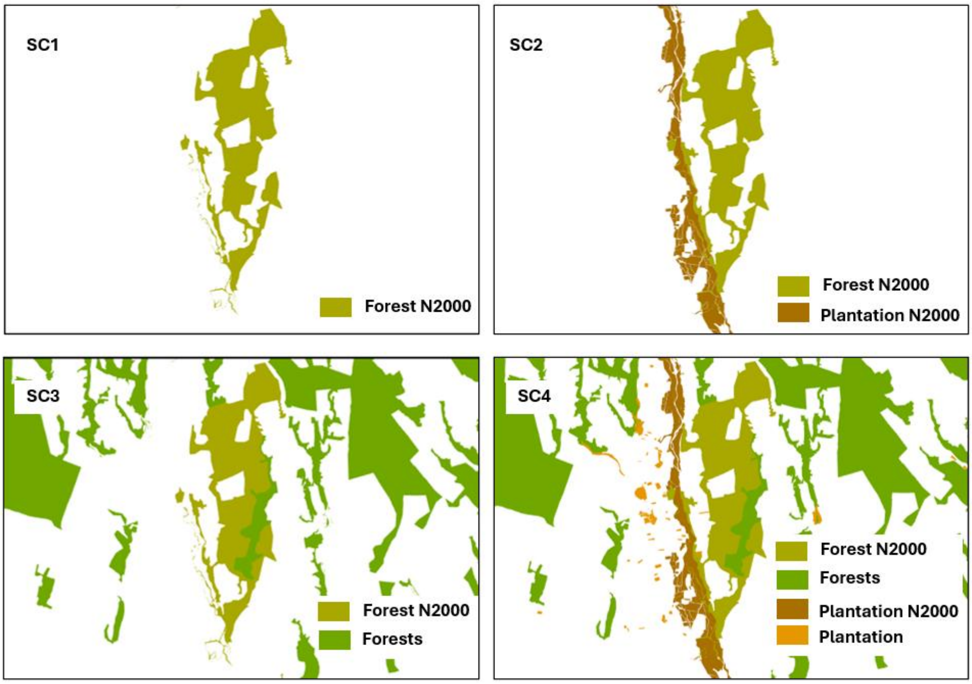

Figure 2. Forest and poplar plantation patches for each scenario. Scenarios 1 and 3 considered only forest patches, while scenarios 2 and 4 additionally included poplar plantations; scenarios 1 and 2 were restricted to patches within Natura 2000 sites, whereas scenarios 3 and 4 encompassed the full study area.

Connectivity was estimated using *Conefor* (command line v2.6) through two complementary metrics: the Probability of Connectivity (Eq 2) (Saura and Pascual-Hortal 2007) and the Equivalent Connected Area (Eq 3) (Saura et al. 2011). Connections between patches were characterized by edge-to-edge Euclidean distances. Interpatch distances were converted to connection probabilities using a negative exponential function, with the median natal dispersal distance associated with a probability of 0.5.

$$\boldsymbol{PC} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^*}{{A_L}^2} \qquad \text{(Eq 2)}$$

$$\boldsymbol{ECA} = \sqrt{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^*} \qquad \text{(Eq 3)}$$

Where a_i and a_j correspond to the areas of nodes i and j, weighted by the habitat suitability of each species (Si-moussi and Thuiller 2024), and A_L is the total landscape area. p_{ij}^* is the maximum product probability of all possible paths between patches i and j. The nodes in this study correspond to individual polygons of forests and plantations within each scenario. The relative change in connectivity between scenarios was expressed as dECA, which is the difference between the final and initial ECA values divided by the initial value. The same approach was applied to calculate the change in habitat suitability-weighted patch area (dA) when new patches were added between scenarios.

In addition to functional connectivity analysis, we assessed structural connectivity for **Study III** to be incorporated as a spatial feature in the prioritization analysis. Structural connectivity was calculated using the circuit theory-based software *Omniscape.jl* (Landau et al. 2021). To reflect the permeability of the landscape, we built a resistance layer based on CORINE land cover riparian classes (European Environment Agency 2021b). Lower resistance values were assigned to natural land covers (such as forests), while higher values were given to more heavily modified classes (such as built or constructed areas).

Together, the functional and structural connectivity approaches provide complementary insights into how plantations influence ecological networks.

Spatial optimization

For **Study III,** we carried out a spatial optimization through the R package *multiscape* (Salgado-Rojas et al. 2026) to optimize the allocation of management actions across the landscape. The aim was to maximize the economic return of commercial poplar plantations while meeting different targets for ecosystem services, structural connectivity, and riparian habitats of community interest.

Each unit in the landscape — both poplar plantations and riparian forests — was assigned one management action. Plantations could be harvested, sustainably managed, or conserved, while riparian forest units were restricted to conservation only.

The optimization was formulated as a mixed-integer linear programming (MILP) model, where profit was maximized subject to minimum ecological retention constraints. Four scenarios of increasing conservation stringency were compared: business as usual (BAU), compliance, riparian, and multifunctional. To enable comparison across distinct features, all feature layers were normalized to a 0–1 range before optimization, and each feature's provision in the resulting scenarios is expressed as a percentage of its baseline value, which corresponds to the total summed provision across all planning units. This allowed us to evaluate the trade-offs between economic returns and ecological provision across the study area. Full mathematical details are provided in the methods section of **Study III**.

RESULTS

The results follow a structured logic, addressing different but complementary dimensions of biomass systems. At the European scale, we first identify the potential of key species to diversify surrounding landscapes. We then narrow our focus to agricultural landscapes, exploring how poplar plantations contribute to functional connectivity for forest bird species. Finally, we demonstrate how management actions can be strategically allocated to maximize economic return and connectivity potential alongside the broader ecosystem services that plantations and forests can provide.

Potential of biomass systems in diversifying land uses in Europe

A total of 426,783 fields and stands of biomass systems were recorded and characterized across 17 European countries, covering over 2.1 million hectares. Eucalypt and radiata pine were recorded only in the Iberian Peninsula, whereas willow was largely confined to northern Europe, particularly Denmark and Sweden. Poplar presented the widest distribution, located from south-western Europe to Scandinavia. Finally, perennial grasses covered mainly central and southern Europe, with miscanthus being the main species, while reed canary grass was relegated to northern regions (Figure 3).

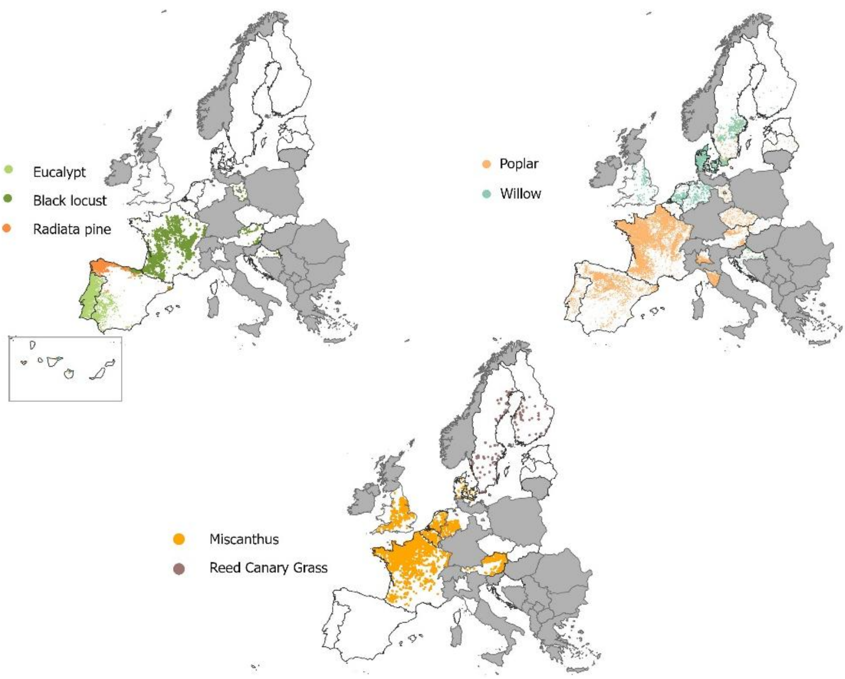

Figure 3. Centroids of stands and fields of biomass systems. Gray areas: No data available

The potential contribution of these systems to land use diversity varied substantially across species (Figure 4). Willow plantations showed the highest potential for enhancing land use diversity, with 57% of all stands located in highly agricultural landscapes, where the introduction of woody elements can have a meaningful diversification impact. Poplar and black locust followed, with 23% and 19% of their stands, respectively, established in low-diversity, agriculture-dominated areas. In contrast, eucalypt and radiata pine plantations were predominantly established in already forested areas with moderate diversity levels, limiting their additional contribution.

In the case of perennial grasses, around 26% of all reed canary grass fields occurred in homogeneous areas with low agricultural cover, where the introduction of herbaceous perennial vegetation has the potential to enhance landscape diversity in otherwise monotonous land use mosaics. On the other hand, miscanthus fields were largely concentrated in intensively farmed areas with low diversity indices, where their structural similarity to surrounding herbaceous crops limits their capacity to enhance local land use composition.

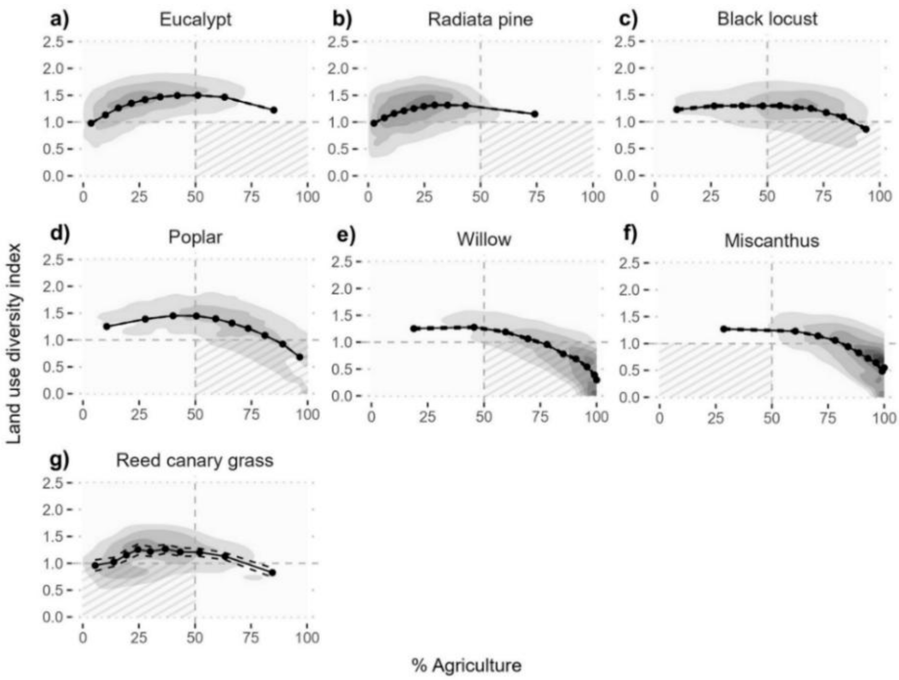

Figure 4. Land use diversity index (LUDI) vs the percentage of agricultural land in the surrounding areas (1 km buffer) of biomass production systems. Filled contour plots represent observation density, ranging from light (low density) to dark (high density). Black dots and dashed lines indicate the 10-tile mean and standard error, respectively. Grey dashed reference lines mark a LUDI of 1 and an agricultural cover threshold of 50%, above which woody plantations and below which perennial grasses are considered to contribute most effectively to land use diversification.

Poplar plantation's role in enhancing functional connectivity

Functional connectivity, measured as the probability of connectivity (PC%), varied considerably across bird species. The Eurasian blackcap (long-dispersal) reached the highest values (~2%), particularly under scenario 4 in both France and Spain, while the common chaffinch consistently showed the lowest values across all scenarios and sub-watersheds (~0.3–0.6%). Adding plantations from scenario 1 to scenario 2 only slightly increased connectivity for all species in Spain, while no evident change was observed in France (Figure 5).

Overall, connectivity gains from adding plantations were greater in Spain than in France, suggesting that existing habitat patches in Spain have a more favorable spatial arrangement for functional connectivity. Furthermore, when plantations were added into the landscape (sc1 to sc2 and sc3 to sc4), connectivity gains consistently surpassed habitat addition in Spain (dECA > dA*suit) across all three species, whereas in France the pattern was more variable and species-dependent (Table 1). The common chaffinch showed higher connectivity gains relative to habitat addition in Spain under sc1 to sc2 (dECA: 8.89% vs. dA*suit: 7.58%), while in France the opposite was true (0.94% vs. 3.67%). This divergence was more pronounced when moving from sc3 to sc4, where the same species in France showed notably higher habitat addition than connectivity gain (21.19% vs. 9.77%), suggesting that newly added habitat in France did not translate into effective connectivity for this short-dispersal species. Similarly, the pattern remained for the great spotted woodpecker and the Eurasian blackcap, where connectivity gains in Spain exceeded habitat addition across both scenario transitions.

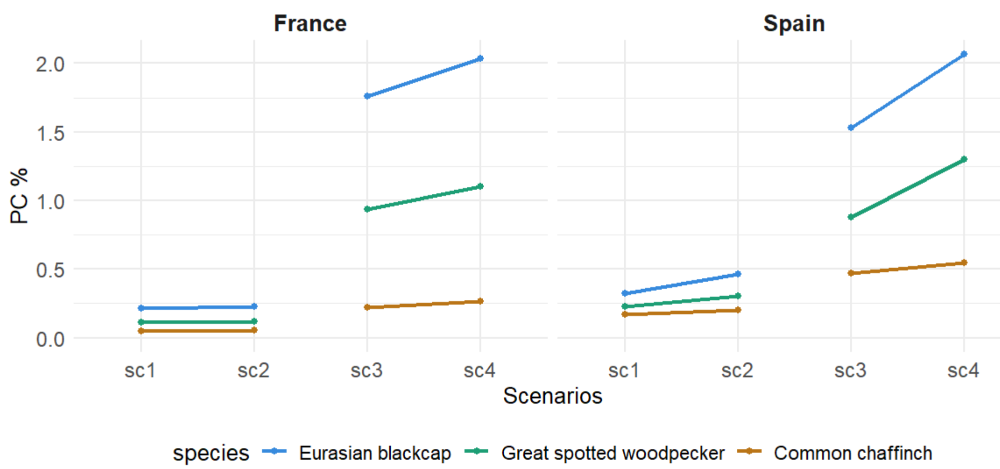

Figure 5. Probability of connectivity (PC %) for sub-catchments in France and Spain for three bird species under four scenarios. sc1: Forests in N2000 areas, sc2: Forests and plantations in N2000 areas, sc3: All forests, sc4: All forests and plantations in the study area.

Table 1. Relative change in connectivity (dECA) and habitat suitability-weighted area (dA*suit) when poplar plantations were added to the network, expressed as a percentage, for each species and country.

Species	Scenario	Country	dECA %	dA*suit %
Common chaffinch ***(Fringilla coelebs*)**	sc-1-sc2	Spain	8.9	7.6
	sc-1-sc2	France	0.9	3.7
	sc3-sc4	Spain	7.9	7.7
	sc3-sc4	France	9.8	21.2
Great spotted woodpecker ***(Dendrocopos major*)**	sc-1-sc2	Spain	15.8	5.7
	sc-1-sc2	France	3.0	2.4
	sc3-sc4	Spain	21.5	4.9
	sc3-sc4	France	8.7	10.0
Eurasian blackcap ***(Sylvia atricapilla)***	sc-1-sc2	Spain	19.6	5.4
	sc-1-sc2	France	2.2	1.8
	sc3-sc4	Spain	16.2	4.2
	sc3-sc4	France	7.4	7.4

Optimization of management actions in poplar plantations

In **Study III**, the spatial distribution of management actions varied substantially across scenarios, with conservation consistently representing the largest share of selected planning units. The number of sustainable management actions remained relatively constant across scenarios, but their spatial distribution differed. In the BAU and compliance scenarios, sustainable plantations were more widely scattered, whereas in the riparian and multifunctional scenarios, they became more concentrated, particularly along riparian areas in the northern part of the study area (Figure 6).

Regarding the provision of features (ecosystem services and connectivity), the BAU scenario resulted in very low levels compared to the baseline, including carbon sequestration (1.8% of baseline), soil retention (1.2%), and connectivity (5.8%). In contrast, the riparian and multifunctional scenarios recovered a substantial proportion of these values, achieving near-baseline levels for multiple services.

Transitioning from BAU to the compliance scenario resulted in a minimal profit loss of approximately €86, suggesting that regulatory conservation targets are compatible with commercial wood production. However, more ambitious conservation targets (riparian and multifunctional scenarios) led to a more substantial profit reduction of approximately 26% relative to BAU. Notably, despite this cost, the riparian scenario achieved the greatest gains across connectivity and habitat features, while retaining values close to the baseline across all ecosystem services. The multifunctional scenario achieved comparable profit levels to the riparian scenario but with slightly lower performance across most features (Table 2).

Further sensitivity analysis confirmed that while moderate conservation targets are achievable at minimal economic cost, profit declines sharply once targets exceed 50%.

Table 2. Summary of the four management scenarios — Business as Usual (BAU), Compliance, Riparian, and Multifunctional — showing the number of planning units (PUs) selected out of 1,730, each feature's provision as a percentage of total baseline provision across all PUs, and net profit (€/year).

	Baseline	BAU	Compliance	Riparian	Multifunctional
Number of planning units					
Conservation	—	314	606	1101	1302
Harvest	—	261	261	218	224
Sustainable	—	24	23	36	30
Ecosystem services					
Carbon sequestration	4225.5	1.8	30	84.4	80
Flood control	65.7	13.4	31.1	72.5	80
Soil retention	776.5	1.2	38.5	94.2	89.2
Riparian habitats					
T11	2496.2	3.0	30.7	81.9	80.0
T12	4412.9	1.2	33.4	88.6	86.4
T13	837.5	2.0	30.0	80.0	80.0
T14	1094.3	3.6	30.0	80.0	81.2
Connectivity	2899.9	5.8	33.9	90.0	81.2
Economics					
Net profit (€)	—	2025272	2025186	1492675	1487002

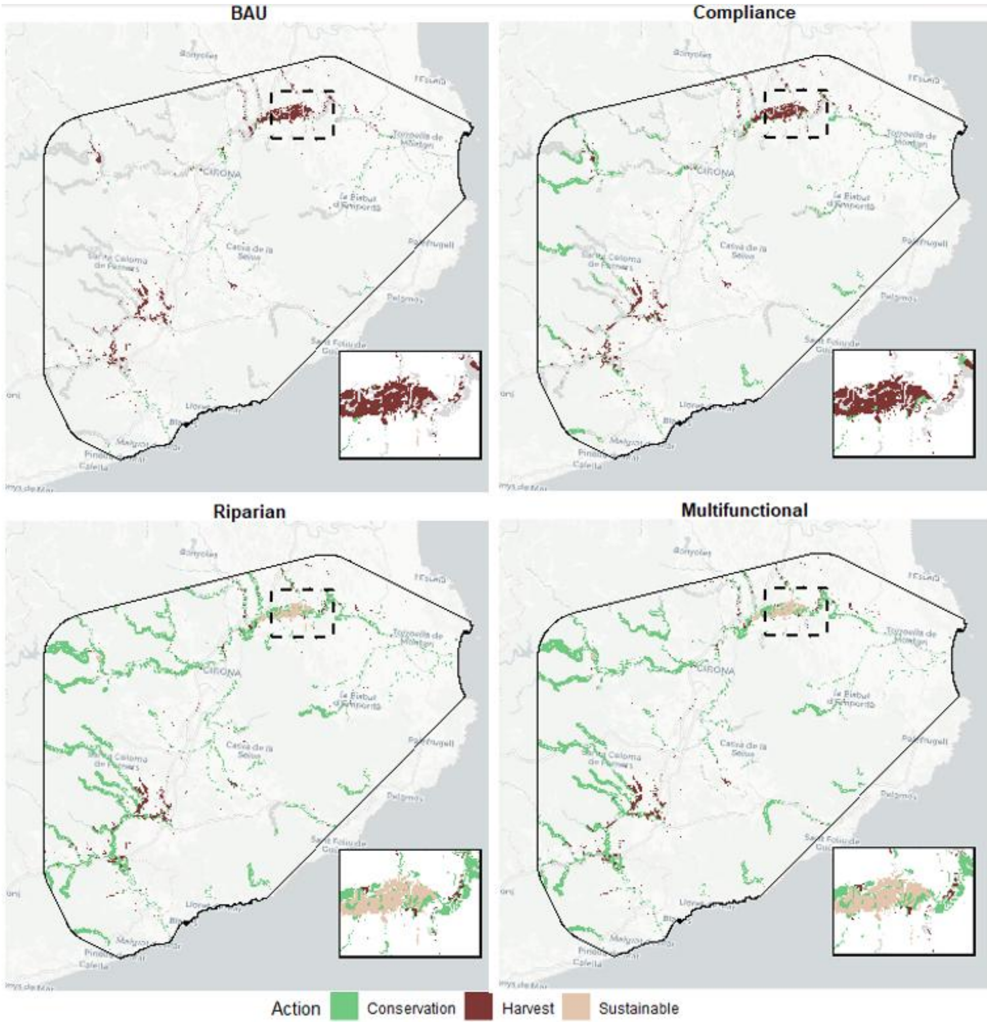

Figure 6. Spatial allocation of actions across scenarios: Business as usual (BAU), Compliance, Riparian, Multifunctional

DISCUSSION

This thesis demonstrates that the potential of biomass systems to support ecosystem services and ecological connectivity highly depends on the spatial context. Their location, surrounding land uses, and ultimately management actions can determine their functional value. By exploring these dimensions, this thesis provides a spatially explicit framework for evaluating and optimizing the ecological contribution of biomass systems in European landscapes, with implications for both land use planning and conservation policy.

Spatial drivers of biomass system impacts

The spatial dimension of biomass systems expansion has received increasing attention, particularly regarding the location of fields and stands. In their perspective article, Van Der Hilst, (2018) highlighted the relevance of site selection when deploying biomass crops for energy, arguing that site-specific characteristics can substantially influence both the economic and environmental sustainability of biomass supply. Consistent with this research interest, in their doctoral thesis, Xu, (2023) examined how energy crop cultivation in Sweden shifted spatially and temporally, revealing the displacement of traditional crops and providing insights into the land-use decisions of farmers and land managers.

Beyond location, the scale at which biomass systems are deployed also plays a key role in determining their impact. Large-scale deployment of short-rotation plantations poses the risk of landscape homogenization, which in turn can be responsible for biodiversity loss (Vanbeveren and Ceulemans 2019). Specifically, large monocultures of exotic trees, such as *Eucalypt spp.*, have been shown to be detrimental to bird diversity (Castaño-Villa et al. 2019; Iglesias-Carrasco et al. 2025). In the Iberian Peninsula, the negative effects of eucalypt plantations have been extensively documented, with the main challenges being their high susceptibility to disturbances (e.g., pests, fires), biodiversity loss, and invasion risk (Tomé et al. 2021). In line with these concerns, in **Study I,** we showed that large *Eucalyptus spp*. stands exceeding 50 ha (Figure 5a in **Study I**) are predominantly located in Portugal and Spain, a pattern reflecting the conservation challenges associated with the scale and spatial concentration of this species in the region.

Another key factor determining the impact of plantations on biodiversity is surrounding land uses. When planted in agriculturally dominant landscapes, biomass systems offer woody elements that can complement the function of natural forest remnants by providing habitat to different species (Brockerhoff et al. 2008). Similarly, Berg, (2002) showed the important effects that adjacent habitat had on bird communities, emphasizing that SRC of *Salix* plantations offer more habitat opportunities in farmland landscapes compared to forested ones. These findings underscore the importance of adopting a spatially explicit approach when evaluating the potential of biomass systems in enhancing biodiversity, as well as considering the broader landscape mosaic in which these systems are embedded. Diverse landscape mosaics have been recognized not only for being beneficial for biodiversity, but also as a key strategy for reducing wildfire risk and pest outbreaks, two growing concerns in the context of climate change (Tomé et al. 2021). Furthermore, landscape diversification through biomass systems can offer farmers alternative income sources, reducing economic dependence on single crops and increasing overall farm resilience (Hauk et al. 2017).

Study I addresses this by characterizing the land use diversity surrounding biomass systems across Europe, identifying which species and locations hold the greatest potential to contribute to land use diversification at a European scale (Figure 5b in **Study I**). It thus provides a spatially explicit framework that can guide the strategic deployment of biomass systems in landscapes where their ecological and socioeconomic potential is most likely to be realized.

The role of biomass systems in shaping ecological connectivity

In addition to diversifying land uses and influencing species composition, SRP can enhance connectivity among isolated forest patches in fragmented agricultural landscapes (Brockerhoff et al. 2008). Early studies suggested that hybrid poplar plantations can enhance connectivity among forest patches, while noting that they are unable to fully support the bird communities characteristic of natural forests (Hanowski et al. 1997). Similarly, Campbell et al., 2012 highlights the role of willow plantations as stepping stones for birds to move between habitat patches that better meet their ecological requirements.

We demonstrated that poplar plantations can enhance functional connectivity for forest birds, emphasizing that spatial configuration and species dispersal capacities play a key role in determining the effectiveness of their contribution to connectivity (**Study II**). These findings are consistent with a growing body of evidence highlighting the influence of woody habitat spatial arrangement and patch shape on landscape connectivity (Madrid et al. 2026; Marcantonio et al. 2024). We further showed that small poplar plantation patches can act as steppingstones connecting key forest patches within the Natura 2000 network, particularly when positioned along riparian corridors. This role has also been recognized for small woody patches in agroecosystems more broadly (Cadavid-Florez et al. 2020). Beyond birds, the connectivity potential of poplar plantations has also been explored for small forest-dwelling species such as the hazel dormouse (*Muscardinus avellanarius*), suggesting that hedgerow-style designs could form part of new movement corridors in fragmented landscapes (Dondina et al. 2018).

It is important to highlight, however, that SRP do not represent optimal habitats for all taxa, and their benefits are largely restricted to generalist species (Vanbeveren and Ceulemans 2019). This was confirmed by the species review conducted for **Study II**, which showed that the bird species most reported in SRP were predominantly forest generalists rather than specialists. Indeed, the expansion of biomass plantations can pose an additional threat to open habitat species such as farmland birds (Zitzmann and Langhof 2023), by displacing the open territories on which these species depend. These contrasting responses highlight the importance of focusing on specific taxa and their traits and habitat preferences when evaluating the ecological effects of plantation expansion, as generalizations across species groups can mask important trade-offs that have direct implications for landscape planning. Furthermore, the enhancement of ecological connectivity won’t be achieved solely by prioritizing the spatial configuration of habitat patches, but restoration actions must be put in place, especially in Spain and France (Saura et al. 2018). This would further facilitate movement to forest species in highly fragmented landscapes.

Creating more connected landscapes and restoring biodiversity are among the most pressing conservation goals of the European Union, reflected in a series of ambitious commitments. For instance, the EU Biodiversity strategy set the target for member states to protect 30% of EU land and restore degraded ecosystems. Furthermore, the recently adopted EU Nature restoration law legally binds countries to restore key habitats such as riverine ecosystems, as well as improve biodiversity indicators in agricultural landscapes (Regulation EU 2024/1991). To meet these targets, expanding protected area networks alone is insufficient, and complementary approaches are also needed. One of such approaches is the Green Infrastructure, a network of natural and semi-natural areas designed to enhance connectivity and deliver ecosystem services (European Commission 2013). Riparian habitats are central to this framework, as they naturally link terrestrial and aquatic ecosystems and are explicitly targeted for restoration under the Nature Restoration Law. The findings of **Study II** are directly relevant in this context; poplar plantations strategically positioned along watercourses can complement natural riparian networks, acting as structural elements that extend Green Infrastructure connectivity into intensively managed agricultural landscapes where natural corridors are often fragmented or degraded. However, this is highly dependent on how these plantations are managed. While biomass systems cannot substitute for natural habitats, strategically located and well-managed plantations can play a meaningful role in supporting conservation strategies.

Management and policy implications

As conservation targets become more ambitious alongside growing demands for biomass and bio-based products, balancing these competing pressures requires a shift towards a more multifunctional landscape perspective. In landscapes where plantations coexist with high-value habitats such as riparian forests, adopting differentiated and sustainable management strategies for biomass systems becomes particularly critical. **Study III** directly addresses this challenge by exploring how management actions can be spatially prioritized in predominantly forested landscapes where poplar plantations coexist with riparian forests, which constitute habitats of high conservation value that are central to river restoration targets.

Using a spatial prioritization framework, we were able to allocate management actions through increasing conservation targets that maximize economic returns from poplar plantations while maintaining ecosystem services provision. Notably, in **Study III**, the riparian scenario achieved the greatest improvements in connectivity and riparian habitat conservation while remaining more cost-effective than the multifunctional scenario. Although the two scenarios differed in their targets, with the riparian scenario prioritizing connectivity and riparian habitats over ecosystem services, this result suggests that spatially targeted conservation actions focused on a specific set of objectives can be economically competitive with broader, more ambitious strategies. This has important implications for conservation planning, as it demonstrates that well-targeted interventions do not need to come at a greater cost. Furthermore, we identified poplar plantations overlapping habitats of community interest, and among all features included in the prioritization, the temperate hardwood riparian forest habitat (T13) was associated with the steepest profit loss. This further reinforces the tension between biomass production and conservation of riparian ecosystems, which highlights the need for adopting sustainable management approaches, especially in plantations coexisting with these sensitive ecosystems.

In practice, sustainable management can include actions such as the reduction of pesticides in favor of biocontrol practices, the adoption of multi-age plantations with different harvesting cycles and allowing the growth of understory vegetation after plantation establishment (Firbank 2008; Rowe et al. 2009). Additionally, mixed-species plantations have been shown to significantly enhance species richness, understory plant cover and biomass, and soil health compared to monocultures (Guo et al. 2025). However, evidence on the mechanisms determining if a mixture will outperform monocultures is still scarce for fast-growing plantations (Thomas et al. 2021). Beyond within-stand management, the integration of fast-growing species such as poplar into agroforestry systems shows a promising future. When poplar plantations are part of silvopastoral systems, intercropping and as hedgerows, they can deliver benefits for biodiversity, carbon sequestration, and biomass production. However, there are still socioeconomic barriers as well as insufficient understanding of tree crop interactions that further limit the adoption of these types of systems (Enescu et al. 2025).

Overall, our results across studies underscore the need to bridge the gap between research and landscape planning. A lack of knowledge about the benefits of SRP has been repeatedly identified as a key barrier to SRP adoption across Europe (Lindegaard et al. 2016), and clearer scientific evidence on the spatial effects and multifunctional potential of biomass deployment could directly inform policy frameworks and economic incentive structures that support their expansion. Furthermore, we suggest that policy measures such as the CAP can include spatially targeted measures for farmers to increase overall connectivity of agroecosystems. Notably, agri-environmental schemes under the current CAP framework offer a promising avenue for the sustainable integration of SRC into agricultural landscapes. However, the implementation of ecological management guidelines remains voluntary and uncompensated, meaning that farmers must assume yield losses or additional management costs. As a result, sustainably managed SRC remains rare in practice (Zitzmann and Rode 2021). Working towards the economic compensation of these practices can be an important concrete step to unlock the multifunctional potential of biomass systems. That said, these policy instruments remain more directly applicable to extensively managed SRC than to the productive fast-growing plantations characteristic of the biomass systems in **Studies II** and **III**. Extending these incentive mechanisms to the latter will require complementary market-based instruments, sector-specific policy frameworks, and a stronger evidence base linking productive plantation management to biodiversity and ecosystem service outcomes, which is precisely where this thesis aimed to contribute.

Future directions and perspectives

Although biomass systems offer a pathway towards climate change mitigation and energy security, their environmental and socioeconomic impacts remain subject to debate. One key factor of this debate, among many others, is the lack of centralized databases that allow for the systematic assessment of their benefits and drawbacks, as well as the absence of harmonized terminology within the sector (Lindegaard et al. 2016). Thus, advancing towards a European-scale biomass monitoring system that gathers data on location, species, management, and ecological outcomes will allow farmers and land use planners to consider the full range of possibilities and make informed decisions for a more sustainable deployment.

In the context of sustainable deployment, this thesis also highlighted the importance of surrounding landscape composition in determining the ecological value of biomass systems. In **Study I**, land cover data were used as a proxy to identify species and locations with the greatest potential to diversify land uses (Figure 5b in **Study I**). Future research could enrich this assessment by incorporating additional dimensions of diversity, such as structural heterogeneity or habitat suitability for specific taxa. In this regard, increasingly accessible remote sensing technologies such as LiDAR offer a promising avenue for characterizing the structural complexity of both biomass systems and their surrounding landscapes, capturing dimensions of ecosystem diversity that land cover data alone cannot reflect. Similar methodological considerations apply to the connectivity analyses presented in **Studies II** and **III**, which relied on modeled rather than empirical representations of landscape connectivity. In **Study II**, connectivity was modeled as potential functional connectivity for three bird species using a graph-theoretical approach based on species-specific dispersal distances and Euclidean distances between patches, without incorporating resistance surfaces to represent matrix permeability. This simplification can underestimate realized connectivity and overlook the importance of barrier effects imposed by other land covers. In **Study III**, connectivity was instead characterized structurally using a circuit theory and used as a feature within a spatial optimization problem; as such, it captures the structural arrangement of habitat patches rather than functional movement potential for any specific taxon.

Despite these differences, both studies share a common drawback: the connectivity patterns identified remain theoretical and have not been empirically validated. A critical next step would therefore be the empirical validation of the connectivity patterns modeled in both studies. While field studies have documented bird communities occurring within SRP, research directly tracking individual bird movement across plantations as steppingstones or corridors in agricultural landscapes remains limited. Individual-based tracking approaches, such as color ringing, mist netting, or telemetry, would provide invaluable ground-truth data to validate model predictions and refine our understanding of how different species interact with these novel landscape elements.

Study III relied on literature-based estimates and expert knowledge to characterize ecological and economic inputs, rather than site-specific measurements. While this enabled a computationally feasible landscape-scale optimization, it simplifies underlying ecological processes by treating feature provision as fixed values rather than stand-specific outcomes. A promising direction for future work would be to complement these inputs with process-based forest models which simulate stand structure and dynamics under different management strategies (De Cáceres et al. 2023), allowing ecosystem service and connectivity provision to be estimated from actual stand conditions.

Furthermore, the effects of biomass systems on ecosystem services and landscape connectivity are likely to be influenced by climate change. In Mediterranean regions, increasing drought frequency threatens the productivity and ecological value of poplar plantations located in riparian areas, some of which draw directly on aquifer tables, potentially adding pressure on water resources. Recent research, for example, has shown that poplar SRC plantations experience significant reductions in leaf area and foliar nutrient concentrations under limited water availability conditions (Fuertes et al. 2023). Thus, identifying and selecting drought-tolerant provenances and genotypes will be critical for ensuring the long-term viability of biomass systems in Mediterranean regions. Additionally, under climate change conditions, the distribution of species will most likely shift, which can alter the connectivity value of plantations and their function as steppingstones, an issue that can be further explored in spatial assessments that integrate climate change projections.

Finally, this thesis provides a static snapshot of biomass systems, and future research can incorporate a multitemporal perspective to understand how their ecological value changes across rotation cycles and management regimes. Biomass plantations are dynamic systems whose functional value can shift substantially between harvest events and as stands mature.

Understanding temporal dynamics is key to designing management schedules that maintain biodiversity and ecosystem service provision continuously across the landscape.

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