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RESEARCH

Strategic placement of plantations enhances forest connectivity for birds in agricultural landscapes

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Abstract
Context Land-use intensification in European agroecosystems has led to the loss and fragmentation of forested habitats, reducing their connectivity. Woody elements within the agricultural matrix play a crucial role in promoting functional connectivity among forest species. In agricultural landscapes, fast-growing plantations represent one such element that is expected to expand in the future due to current EU goals of climate change mitigation and energy security.
Objectives In this study, we aim to assess the potential contribution of poplar plantations in enhancing functional connectivity for forest birds in agricultural landscapes.
Methods To estimate functional connectivity, we conducted a scenario analysis in two agricultural sub-catchments located in Spain and France. Using a graph-based connectivity analysis and three focal forest bird species with different dispersal capacities, we estimated the added value of plantations under four scenarios where forests and plantation patches inside and outside Natura 2000 sites were added progressively.
Results We found that the contribution of plantations to functional connectivity is highly context-specific, depending largely on their spatial configuration and the arrangement of existing forest patches. Plantations were most effective when placed as stepping stones, for example, along river corridors connecting large, forested patches. Thus, simply increasing wooded areas through plantations does not necessarily yield a proportional improvement in connectivity.
Conclusions Expansion of poplar plantation areas and seminatural wooded patches in agroecosystems should explicitly consider the location of their implementation to effectively contribute to functional connectivity. Future policies could consider targeted incentives for the strategic placement of poplar plantations.

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Introduction

Agricultural expansion and intensification are some of the main causes of natural habitat loss and fragmentation (IPBES 2019; Zabel et al. 2019). Although a few studies have questioned the negative effects of habitat fragmentation on biodiversity (Fahrig et al. 2019; Riva and Fahrig 2023) most of the scientific evidence suggests that fragmentation can adversely affect biodiversity at the patch and landscape level (Fletcher et al. 2018; Gonçalves-Souza et al. 2025) leading to biodiversity decline and loss. Generally, in agriculturally dominated landscapes, habitat loss is more pronounced due to the expansion of intensively cultivated areas that drastically reduce the extent and contiguity of non-crop covers such as forests and wetlands. Agricultural intensification increases both the distance between remnant natural habitat patches and the landscape resistance to species dispersal, thereby reducing their functional connectivity at the landscape level (Arntzen et al. 2017). Connectivity is crucial for ensuring the persistence and stability of meta-populations, as well as preserving gene flow and genetic diversity (Lowe and Allendorf 2010; Radford et al. 2021).

Within agricultural landscapes, small woody features become more important to counteract the effects of forest fragmentation. Species depending on forest habitats can make use of woody vegetation patches present in agricultural matrices to find refugia and resources to thrive, as well as to move among remnant forest patches (i.e., as steppingstones). In fact, Marcantonio et al. (2024) showed that the expansion of small woody features in highly agricultural areas in Europe could increase connectivity by 6.5% over existing woody cover in these landscapes. Recognizing the potential role of woody vegetation in farmland biodiversity, recent EU policy frameworks have increasingly promoted their integration into agricultural landscapes. As part of the echo-scheme strategies, the EU's common agricultural policy (CAP) encourages measures that minimize the negative impacts of agriculture on the environment, including the establishment of woody features, such as hedges and rows of trees to enhance biodiversity and contribute to climate change mitigation (European Commission 2019). The 2023–2027 CAP introduced additional incentives for farmers to support the development of agroforestry in the form of short rotation coppice (Geier et al. 2025).

Fast-growing plantations (FGP) are tree systems established with species selected for rapid growth, mainly located within agricultural landscapes (Pineda-Zapata and Mola-Yudego 2025). In Europe, poplar plantations are one of the most widespread and economically significant species, cultivated for several decades to supply a variety of bio-based products, including timber, pulp, fiber, and bioenergy feedstocks (Lindegaard et al. 2016). Although plantations rarely provide the full habitat quality required by forest specialists, empirical studies indicate that, under certain conditions, they can contribute to species movement and functional connectivity for birds. For example Campbell et al. (2012) showed that birds frequently moved between willow plantations and surrounding habitats, suggesting that these stands can be used for foraging and as a complementary habitat within a broader landscape mosaic. However, this use was strongly influenced by plantation age and their location within areas containing herbaceous and woody cover. Similarly, Hanowski et al. (1997) suggested that poplar plantations can be strategically promoted to enhance connectivity among existing forest patches, but that their value for birds depends on both the surrounding land use and plantation age. Likewise, Martín-García et al. (2013) proposed that poplar plantations could improve connectivity among remnant forest patches in Spain, while emphasizing the need to consider the potential negative effects of large-scale afforestation on open-habitat bird communities.

The large-scale deployment of FGP may lead to undesirable effects on biodiversity (Dauber et al. 2010; Tarr et al. 2017): studies based on modeling approaches at the European scale have shown that large-scale biomass production may have a negative effect on reptiles, butterflies, and birds (Eggers et al. 2009; Louette et al. 2010). Species of conservation concern and specialists, such as cavity nesting, have also been reported to be negatively impacted by plantations (Reino et al. 2009; Camprodon et al. 2015). Nevertheless, depending on the land use context, this type of plantation could be beneficial for certain species. Oliveira et al. (2024) found significantly higher fauna-flora richness in short-rotation poplar plantations than in adjacent agricultural land, with fauna showing slightly higher richness values when compared to forested areas. A study from Berg (2002) in Sweden suggests that planting *Salix* in farmlands increases structural diversity, which in turn has positive effects on bird populations. Similarly, Chiatante et al. (2019) demonstrated the complementary value of poplar plantations in connecting isolated forest patches for forest bird species in a highly fragmented landscape. These benefits vary among species and depend on how species respond to landscape properties, with responses shaped by intrinsic traits such as dispersal capacity, mobility, and degree of specialization, which condition how species interact with novel landscape elements (Öckinger et al. 2010).

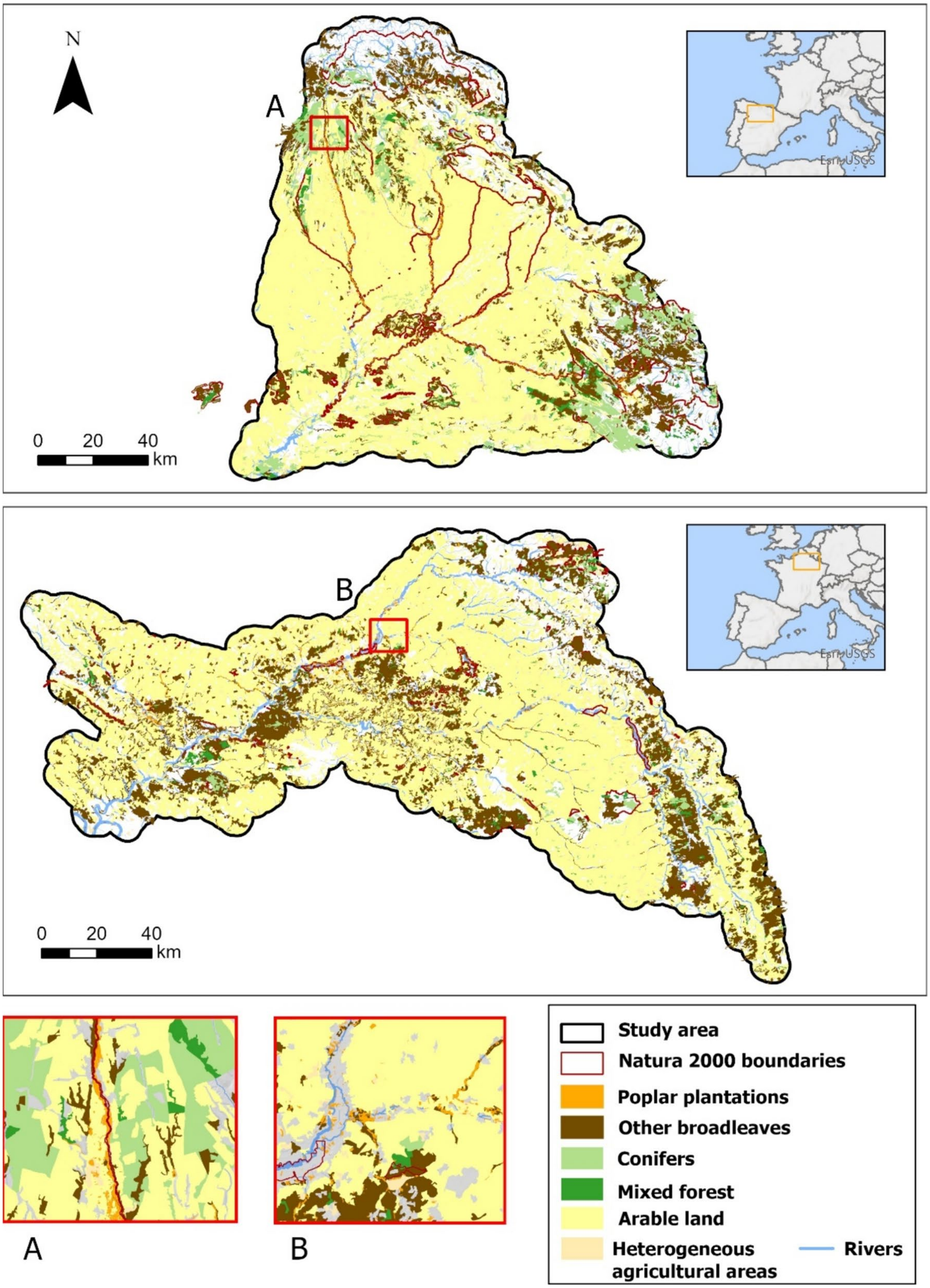
In highly modified landscapes with few forest remnants, suboptimal habitats like FGP can enhance landscape connectivity by acting as semi-natural corridors that link isolated forest patches. These plantations may increase landscape permeability, supporting species movement and survival across agriculture-dominated areas (Dondina et al. 2018; Müller-Kroehling et al. 2020). In this context, the presence of plantations can contribute to enhancing forest connectivity within the existing Natura 2000 (N2000) network of protected areas (PAs), which constitutes the backbone of biodiversity conservation in Europe. To strengthen the connectivity between existing PAs, the European Union has recently adopted the EU Nature Restoration law, which emphasizes the need to improve forest habitat connectivity and restore ecological networks. This regulation builds upon earlier policy frameworks, such as the EU Green Infrastructure initiative launched in 2013, which aimed to integrate natural and semi-natural areas into a cohesive ecological network that supports species movement and adaptation to climate change. Despite these efforts, connectivity within the N2000 network remains insufficient, and increasing the permeability of the matrix surrounding protected areas is considered necessary for effective biodiversity conservation (Saura et al. 2018).

Despite growing interest in enhancing connectivity through multifunctional land uses, the extent to which fast-growing plantations contribute to landscape-scale ecological networks remains relatively unexplored, with early studies suggesting that, depending on the management and surrounding land uses, plantations may facilitate connectivity among forest remnants for birds in fragmented landscapes (Hanowski et al. 1997). Therefore, in this study, we sought to understand the role of poplar plantations in supporting forest connectivity at the landscape scale in agriculturally dominated areas. We focused on evaluating the potential of poplar plantations (assuming their function as stepping stones) to improve the connectivity of forest habitats within and among N2000 areas in two agricultural sub-catchments in Spain and France. First, we revised and compiled a list of bird species reported to be found in both plantations and natural forested areas and selected three forest species that differed in their dispersal capacity. Then, using a graph theory approach, we assessed the net contribution of poplar plantations to forest habitat connectivity across four scenarios where habitat patches, i.e., forests and plantations within and outside N2000 sites, were added progressively. Finally, for each focal species, we quantified the relative contribution of poplar plantations to connectivity by measuring the change in the Equivalent Connected Area (ECA) index between scenarios and ranked individual patches' importance using the Probability of Connectivity Index (dPC). Overall, our study aims to provide insights that can support practical spatial planning and management of poplar plantations in agricultural landscapes to foster forest connectivity.

Methods

Study area

To assess how plantations contribute to the functional connectivity of forest habitats in agricultural landscapes, we selected two sub-catchments in Spain and France corresponding to the Pisuerga and Oise rivers, respectively (Fig. 1). The boundaries for the areas were retrieved from the European catchments and river network system dataset (Ecrins) (European Environment Agency 2012). We selected these sub-catchments because they are dominated by an agricultural land use matrix and the presence of poplar plantations. Agricultural land covers, corresponding to arable land and heterogeneous agricultural areas within the sub-catchments comprise around 1.5 and 1.7 M ha in Spain and France respectively (see Fig. 1).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Study area
Natura 2000 boundaries
Poplar plantations
Other broadleaves
Conifers
Mixed forest
Arable land
Heterogeneous agricultural areas
Rivers

◂**Fig. 1** Maps of study areas showing selected sub-catchments and a 5 km buffer in Spain (top) and France (bottom). Maps depict land cover classes included in the connectivity analyses (forests and poplar plantations). Additionally, agricultural land-use classes are also shown (European Environment Agency 2012). Natura 2000 site boundaries in dark red. Insets A and B show detailed views of highlighted areas in Spain and France, respectively

Within these sub-catchments, we selected N2000 sites, sourced from the Natura 2000 EU database (European Environment Agency 2012). The Natura 2000 network is a set of protected sites across the European Union designated under the Habitats Directive (92/43/EEC) and the Birds Directive (2009/147/EC) to safeguard species and habitats of community importance, while allowing for compatible human activities. Sites may be designated for their habitats, their species, or both. In our study, we specifically selected sites where forested habitats were listed as conservation targets (code 9 in the Habitats Directive 92/43/EEC). However, these sites can also comprise other habitat types such as grasslands and heaths, which are protected under the same framework but were not the focus of our selection criteria.

Some of these forested N2000 sites only partially overlapped with the sub-catchment boundaries; therefore, we included those with more than 70% of their area inside them. Finally, we created a 5 km buffer around sub-catchments and selected N2000 sites to ensure that connectivity of the studied terrestrial habitats, i.e., forests, was assessed, accounting for their coverage beyond the sub-catchment limits; that is, all forests and plantations within these buffers were included in the connectivity analyses.

Mapping plantations and forest patches

Poplar (*Populus* spp.), under different clones and hybrids, is widely used in plantation systems in Europe (Pineda-Zapata and Mola-Yudego 2025). Although such plantation systems are sometimes referred to as Short Rotation Plantations (SRP), in the study area, they are primarily managed for wood production rather than bioenergy and are therefore more accurately described as fast-growing plantations (FGP). At the national scale, estimates suggest that plantations occupy around 80,000 ha in Spain and 194,000 ha in France (Crespo Pinillos and Souto Suárez 2023). The species can have rotation lengths of around 12–17 years or 20 in some cases (Fernández and Hernanz 2004; Archaux and Martin 2009). Poplar plantations typically undergo weed control during the first six years and can display different structural stages throughout their rotation. Between 3 and 7 years, plantations usually have an open canopy, while mature stands aged 8 to 14 years often develop a closed canopy, and herbaceous cover tends to decline sharply (Martín-García et al. 2016).

To retrieve spatial data regarding these, we used the poplar plantation forest map for the Spanish sub-catchment (Ministerio para la Transición Ecológica y el Reto Demográfico 2020). Since there is no official database of poplar plantations in France, we used forests categorized as poplars from the dataset BD Forêt® version 2.0 (IGN 2021). To simplify overly detailed polygons, since they would later be combined with broader-scale data, we merged those separated by less than 10 m, using dilatation-erosion process. Such operations are commonly used to smooth land use data by using a positive buffer followed by a negative buffer of the same radius.

To identify current forest patches, we used the 2018 Corine Land Cover database (European Environment Agency 2012). First, we selected forest polygons of which more than 70% areas intersected the study area and filtered them to retain only those categorized as forested land covers: broadleaved forests (Corine code 311), coniferous forests (Corine code 312), and mixed forests (Corine code 313). These selected polygons were then combined with FGP data to create a unified layer of forest and plantation areas, which we used as habitat patches in our analysis.

Focal species selection

We reviewed scientific literature to identify forest bird species using poplar plantations as habitat or as steppingstones when moving between forest patches across the landscape. From fourteen articles documenting bird species in FGPs across Europe, we selected the most frequently reported species in poplar plantations (See Table S1 for a complete list). Among these, we chose three with different dispersal capacities to represent the variation in how species might move across the landscape. This is crucial because connectivity models strongly depend on species' movement abilities: short-distance species need closely spaced habitat patches, while long distance can reach more isolated patches

(Saura et al. 2014). Dispersal capacities were estimated as the geometric mean of their natal dispersal distances reported in Paradis et al. (1998).

To make the final species selection, we discarded species that did not have a documented dispersal value and that were not reported in both sub-catchments. The latter was informed by revising species occurrence data on the European Bird Atlas maps (EBCC 2022). As a representative of species with limited dispersal range, we selected the common chaffinch (*Fringilla coelebs*), with a mean dispersal distance of 0.79 km. The Great spotted woodpecker (*Dendrocopos major*) was selected to represent medium dispersal distances with a mean value of 5.9 km, and the Eurasian blackcap (*Sylvia atricapilla*) for long dispersal capacity with a mean value of 17.5 km.

Connectivity analysis

We used the graph-theory based software Conefor command line (version 2.6) to measure functional connectivity between habitat patches within each sub-catchment. In our study, potential functional connectivity is understood as the landscape-mediated ease of movement and dispersal of organisms, determined by both species' dispersal capacities and the configuration of forest and plantation patches within the landscape (Martínez-Richart et al. 2024). We focused on two metrics which account for landscape spatial structure, species dispersal ability and habitat quality: the Probability of Connectivity (PC) (Saura and Pascual-Hortal 2007) and the Equivalent Connected Area (ECA) (Saura et al. 2011). The PC metric ranges from 0 (no connections) to 1 (all habitats are connected) and describes the probability that two points in a landscape are reachable within the same habitat patch or through other connected habitat patches (i.e., connection via steppingstones). The ECA, derived from the PC metric, represents the size of a single, fully connected habitat patch that would provide the same connectivity as the existing, fragmented network of habitat patches in the landscape.

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^*}{A_L^2} \quad ECA = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^*}$$

where a_i and a_j are the areas of nodes i and j weighted by the habitat suitability of each species, and A_L refers to the total landscape area. p_{ij}^* is the maximum product probability of all possible paths between patches i and j. Individual polygons of forests and plantations were considered as nodes.

In graph theory approaches, patch area is commonly used as an attribute to represent intra-patch connectivity $\left(a_i a_j\right)$ However, several studies have incorporated habitat quality or heterogeneity attributes to better capture a node's potential to support the focal species (Minor and Urban 2007; Justeau-Allaire et al. 2024). We applied a quality-weighted area by using habitat suitability as a proxy for habitat quality (see e.g. Duflot et al. 2018). Specifically, we extracted the median habitat suitability value for each patch using the *exactextract* package (Daniel Baston 2023), which performs an area-weighted extraction of raster cells intersecting each patch, from a dataset providing predictions of habitat suitability for terrestrial vertebrate species across Europe at a 1 km resolution (Si-moussi and Thuiller 2024). This was done for each of the selected species. Therefore, in our case, the ECA metric represents the size of a single, fully connected patch with the maximum habitat suitability (i.e. equal to 1).

Connections between patches (represented as a link between nodes in the spatial graph) were characterized by edge-to-edge Euclidean distances between the forest and plantation patches (polygons). As our study areas had a large number of patches/nodes (~200–6000), the Conefor input extension in ArcMap was unable to calculate edge to edge distances. Therefore, we implemented parallel processing in the software R (R Core Team 2024) by using the *terra* (Hijmans 2025) and *parallel* packages to run the analyses. Calculating distances for extensive networks such as ours can be computationally expensive, and it may take days or weeks. Thus, to overcome memory and computational power issues, we used the Puhti supercomputer provided by CSC–IT Center for Science (www.csc.fi), Finland, to run batch processing scripts for all scenarios.

To reduce computation time in Conefor, we set a threshold equal to twice the standard deviation of dispersal distances reported in Paradis et al. (1998). This ensured that only connections within a plausible dispersal range for each species were considered, thereby considerably reducing computational needs. To estimate the p_{ij} values, the software automatically converts the interpatch distance (Euclidean distance in our case) to probabilities by using a decreasing exponential function. We used the median natal dispersal distance for the selected species and associated it with a probability of 0.5 (Saura and Pascual-Hortal 2007).

Creation and comparison of scenarios

To evaluate the role of poplar plantations on forest habitat connectivity, we compared four connectivity scenarios. Scenarios 1 and 2 considered forest and poplar plantation patches located within N2000 sites as the only potential connection nodes in our network. Specifically, scenario 1 evaluated functional connectivity considering only natural forest patches within N2000 sites, while scenario 2 also accounted for poplar plantations within these sites. Scenario 3 included all forest patches across the study area, both inside and outside N2000 sites, while scenario 4 accounted for all forests and poplar plantations. Scenario 4 reflects the actual landscape composition and structure and the full availability of forest and plantation patches (see Fig. 2). Summarizing, scenarios 1 and 3 only considered forests, while plantations were added in scenarios 2 and 4 in order to evaluate their contribution to N2000 sites and to the forested network of both sub-catchments.

The relative change in connectivity between scenarios (i.e., when a new set of nodes was added to the landscape), was calculated as the dECA. This is simply the difference between the final and initial ECA values, divided by the initial value. Similarly, the relative change in patch area weighted by habitat suitability was calculated as the difference between scenarios when new patches were added (dA). As we only considered the addition of new habitat patches to the existing landscape (without modifying the matrix), comparing the relative changes in connectivity (dECA) and habitat

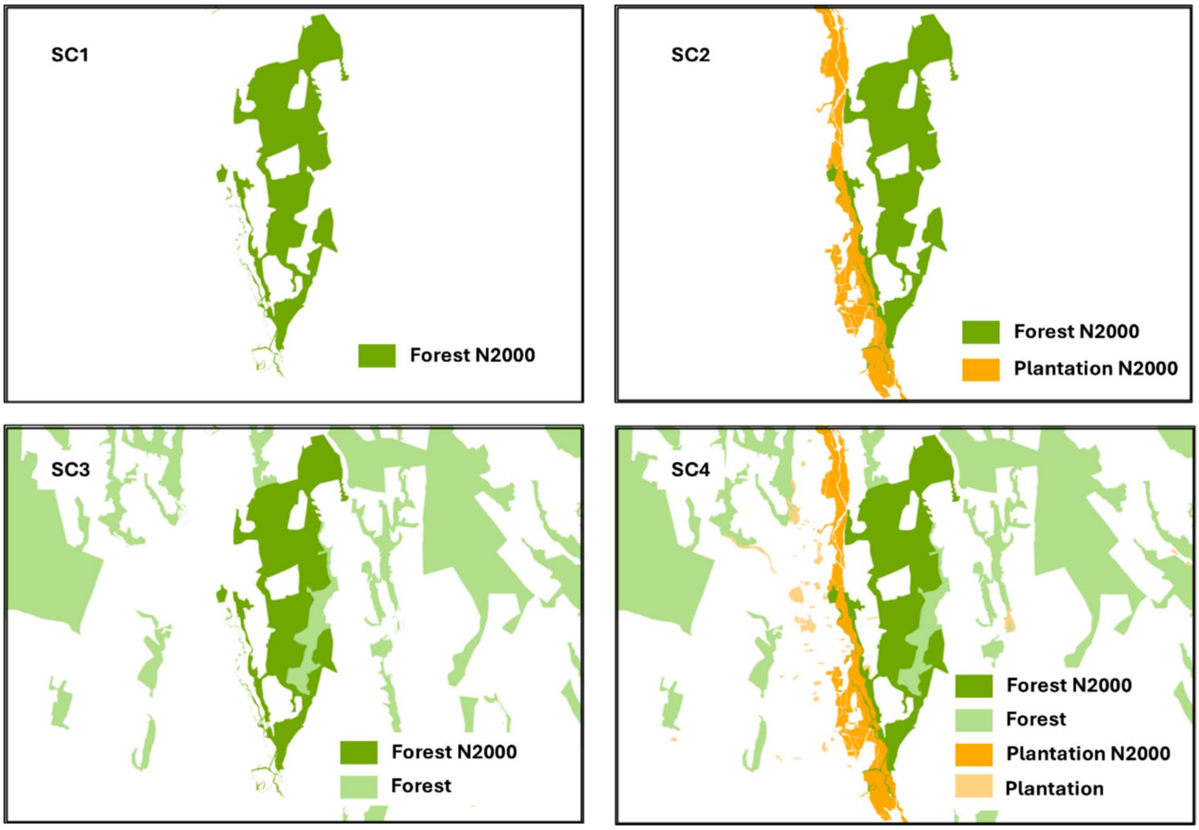

Fig. 2 Description of patches included in each scenario (sc1–sc4) for connectivity analysis. N2000 denotes Natura 2000 sites, *Plantation* refers to poplar plantations under that scenario

area (dA) can offer insight into how spatially efficient those changes are (Saura et al. 2011). If dECA < dA, the new patches contributed less than expected to connectivity based on their area, perhaps because they were highly isolated and do not work as effective connectors. On the other hand, if dECA > dA, the new patches improve connectivity of other patches, likely because they are acting as steppingstones or are part of corridors between existing habitat patches. Finally, if dECA = dA there is a neutral effect when new patches are added, this might be the case when the patch added is adjacent to an existing one. Still, in that latter case, habitat availability increases.

Additionally, we assessed the contribution of each habitat patch to overall connectivity. This was calculated as the percentage of the variation in PC (dPC_k), that is the proportional reduction of PC when element k is removed from the landscape. This was only applied to scenarios 1 and 2 due to computational constraints caused by the large number of nodes in scenarios 3 and 4.

$$dPC_k = \frac{PC - PC_{remove,k}}{PC} * 100$$

Results

The selected forest patches accounted for 19% of the total area in both sub-catchments, while poplar plantations represented less than 1%. Forests and plantations were distributed across more than 4500 patches in Spain and over 6500 in France (Table 1). The size of the patches was highly variable, with mean values around 219 ha (± 864 ha) and 4 ha (± 18 ha) for forests and plantations, respectively, in Spain. In France, mean patch areas were similar, around 214 (± 966 ha) and 5 ha (± 13 ha) for forests and plantations, respectively (see Figure S1).

Functional connectivity (PC) values increased with species' dispersal capacities in both sub-catchments. Across all scenarios, the highest connectivity values were found for the Eurasian blackcap (high dispersal capacity), followed by the great spotted woodpecker (medium dispersal capacity) and the common chaffinch. Under the most complete scenario, considering all forests and plantation patches (sc4), maximum PC values reached around 2% for blackcap, and remain below 0.6% for the chaffinch (low dispersal capacity) (Fig. 3).

Connectivity under scenario sc1 (only forest patches in N2000) was, in general, low for both sub-catchments (< 0.5), but slightly higher in Spain across all species. Adding plantations to N2000 forest patches (sc2) resulted in connectivity slightly

Table 1 Descriptive statistics of the landscape features for the two sub-catchments and across scenarios

		Spain		France
Total sub-catchment area (M ha)*		1.9		2.2
Natura 2000 sites**		14%		21%
Plantations**		0.6%		1.1%
Forest**		19%		19%
Scenarios	N patches†	Area (M ha)	N patches†	Area (M ha)
sc1	530	0.177	212	0.175
sc2	1153	0.184	434	0.177
sc3	1656	0.363	1941	0.416
sc4	4599	0.375	6557	0.440

sc1: Forests intersecting N2000 sites, sc2: Forests and plantations intersecting N2000 areas, sc3: All forests, sc4: All forests and plantations

*M ha: millions of hectares

**Percentage relative to total sub-catchment area

†Number of patches considered in each scenario for the analysis

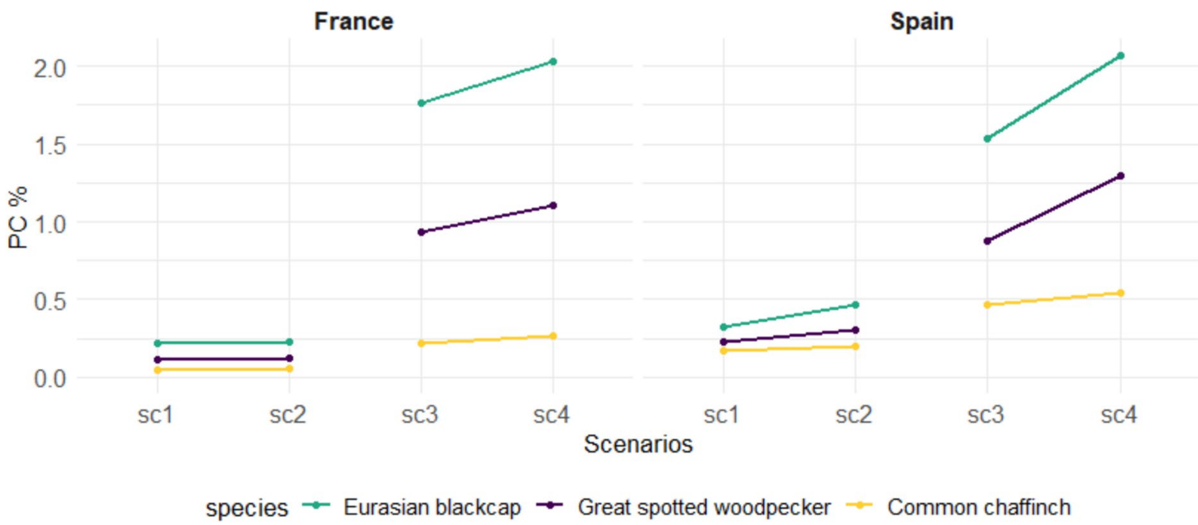

Fig. 3 Probability of connectivity values (PC %) for both sub watershed in Spain (left side) and France (right side) for the three selected bird species under the four scenarios analyzed: sc1: Forests intersecting N2000 areas, sc2: Forests and plantations intersecting N2000 areas, sc3: All forests, sc4: All forests and plantations

increasing for all species in Spain, while for France, adding these patches had little to no effect (Fig. 3).

Despite having less overall forested area in sc3 (see Table 1), the Spanish sub-catchment had higher connectivity (PC) values than the French one for the common chaffinch. In contrast, for the woodpecker and blackcap, PC values were slightly higher in France under the same scenario (Fig. 3). This would suggest a more favorable spatial arrangement of patches for short-distance movements in the Spanish sub-catchment. A similar pattern occurred for sc4, when all forest and plantation patches were considered. This means that plantations in Spain are spatially positioned in a way that enhances connectivity (e.g., bridging key areas), while in France, they contribute more to habitat area than network structure.

Relative contribution of poplar plantations to functional connectivity (dECA)

The relative contribution of poplar plantations to landscape connectivity (scenarios 2 and 4 compared to scenarios 1 and 3, respectively) highly reflected differences between dispersal capacities, as well as landscape structure between the two catchments. The greatest contribution of plantations to increase functional connectivity (dECA) was for the great spotted woodpecker (medium dispersal capacity) under scenario 4 in the Spanish sub-catchment, with 21.6% (Table 2). In contrast, the smallest connectivity increase among all species and scenarios was recorded in France for the common chaffinch under scenario 2, at just 0.94%.

The comparison between changes in connectivity (dECA) and habitat availability (dA*suitability) highlighted species-specific and spatially variable effects (Table 2). In Spain, the addition of plantations generated connectivity gains that exceeded their habitat area across all species and scenarios (dECA > dA*suitability), which suggests that when introduced in the landscape, plantations contributed more to connectivity than to total available habitat. In France, the opposite trend was generally observed (dECA < dA*suitability), indicating that plantation patches were more isolated and less effective in enhancing overall functional connectivity than in Spain. An exception was found for the Eurasian blackcap under scenario 4, where both metrics were nearly equal (7.40 and 7.45%, respectively), that is, plantations are relatively well connected on average, but did not improve the overall connectivity of the forest habitat network.

Table 2 Relative variation of dECA and area weighted by habitat suitability (dA*suit) for each species in scenarios where plantations were added; sc1–sc2: when plantations are added to existing N2000 forested areas, and sc3–sc4: when plantations are added to all forested patches (most complete scenario)

Species	Scenario	Country	dECA %	dA*suit %
Common chaffinch (0.79 km) *(Fringilla coelebs)*	sc–1–sc2	Spain	8.89	7.58
	sc–1–sc2	France	0.94	3.67
	sc3–sc4	Spain	7.88	7.66
	sc3–sc4	France	9.77	21.19
Great spotted woodpecker (5.9 km) *(Dendrocopos major)*	sc–1–sc2	Spain	15.81	5.67
	sc–1–sc2	France	3.03	2.42
	sc3–sc4	Spain	21.55	4.90
	sc3–sc4	France	8.72	10.07
Eurasian blackcap (17.5 km) *(Sylvia atricapilla)*	sc–1–sc2	Spain	19.64	5.37
	sc–1–sc2	France	2.18	1.76
	sc3–sc4	Spain	16.17	4.18
	sc3–sc4	France	7.40	7.45

Individual node importance for forests and plantations intersecting N2000 sites

To understand the contribution of individual nodes to functional connectivity within N2000 sites, we assessed their importance using the dPC metric. For clarity, we focus here on the most contrasting results from the largest dispersal distance species, the Eurasian blackcap. Rankings of dPC values for the other two species are provided in Figure S2 and Figure S3 in the supplementary material.

In Spain, plantations contributed approximately 14% to the total dPC (sum of dPC across all patches), while forest patches accounted for about 86%. This difference was even more pronounced in France, where forest patches contributed 99% of the total dPC, and plantations only around 1%. The nodes with the greatest contribution to overall connectivity (highest dPC values) were two broadleaf forest patches in eastern Spain, located in La Sierra de la Demanda and Sabinares del Arlanza, with dPC values of 28.6 and 21.2, respectively. In France, several habitat patches with high dPC values were found near the center of the study area, intersecting the Massif forestier de Compiègne and Massif forestier de Saint-Gobain, with values around 39.7, and 30.1 respectively (Fig. 4).

When assessing the importance of individual nodes for the common chaffinch (short dispersal distance) we found that, in Spain, the maximum dPC values were higher compared to those for the Eurasian blackcap *Eurasian blackcap* (Figure S2). However, nodes located in the central part of the Spanish study area had very low importance for the chaffinch (dPC: 0–0.92), especially when compared to the same patches for the blackcap (dPC > 1.98), which has the greatest dispersal capability among the studied species.

Discussion

In this study, we assessed the contribution of poplar plantations to enhance forest connectivity of the current Natura 2000 (N2000) network and across two agricultural sub-catchments in Spain and France. Our results show that the contribution of plantations to functional connectivity is highly dependent on both the spatial arrangement of habitat patches and the dispersal abilities of the species. We found that plantations significantly increase forest connectivity, particularly for species with intermediate to long dispersal capacities. However, this contribution varied greatly between the two sub-catchments, despite their similar total forest area.

Differences in functional connectivity among species and sub-catchments

We found that plantations can enhance functional connectivity, but the effect varied strongly with species' dispersal capacity. Overall functional connectivity (PC%) was consistently higher across scenarios for species with moderate and long dispersal abilities, i.e., the Great spotted woodpecker and the Eurasian blackcap, respectively (see Fig. 3). As expected, for

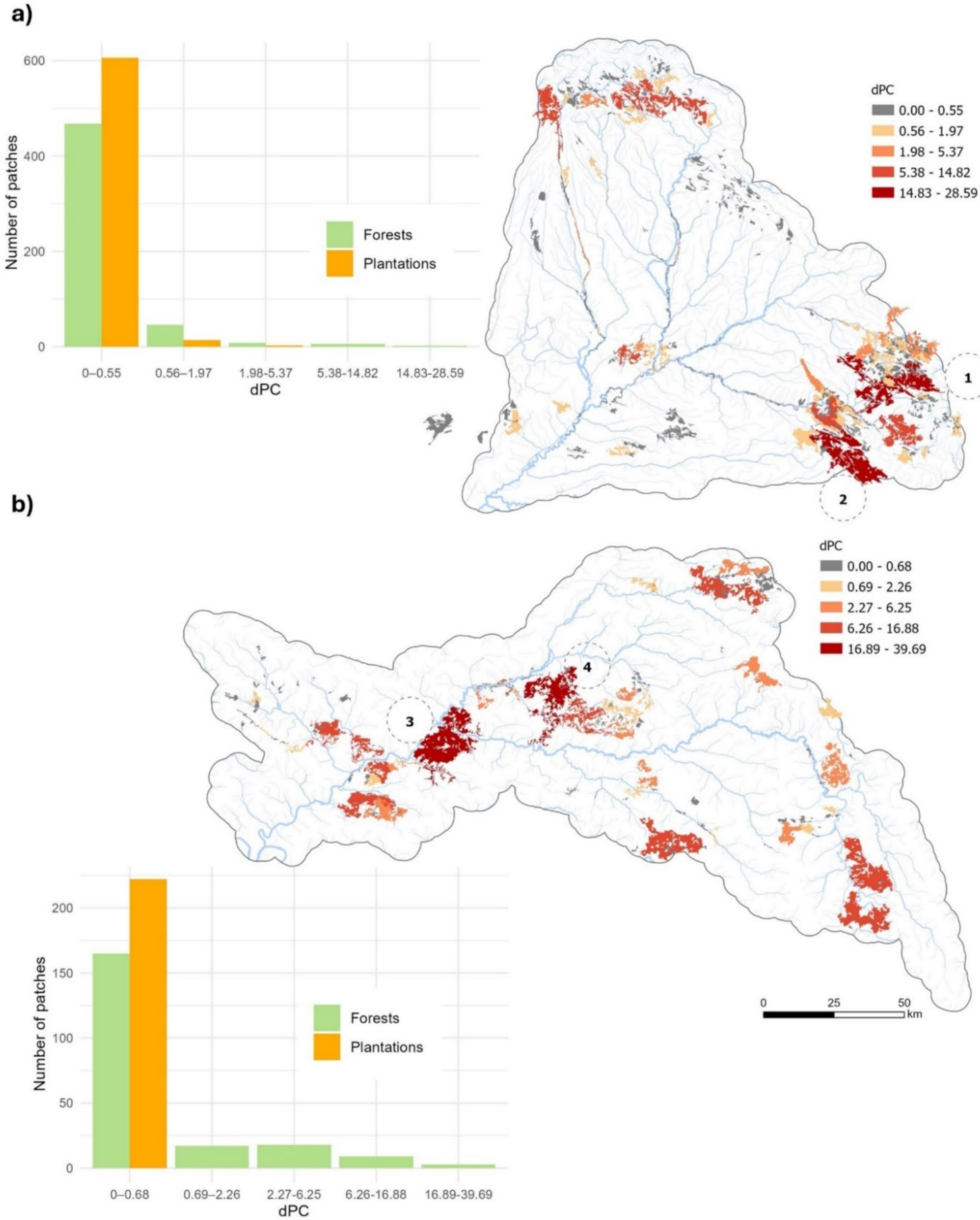

Fig. 4 Frequency histogram and maps of node importance (dPC) for scenario 2 (forests and plantations intersecting N2000 areas) in **a** Spain and **b** France using a median dispersal distance of 17.5 km (Eurasian blackcap). Darker red colors represent patches with higher importance to maintain landscape connectivity. Numbered circles correspond to forest patches intersecting the N2000 sites of 1. La Sierra de la Demanda, 2. Sabinares de Arlanza, 3. Massif forestier de Compiègne, 4. Massif forestier de Saint-Gobain. dPC classes were defined using the Natural Breaks (Jenks) method in ArcGIS

short dispersal species such as the chaffinch, poplar plantations made little difference (Table 2) because many forest patches remained beyond their dispersal range. For these species, FGP may only improve connectivity when planted as close-range stepping stones (< 1 km). Furthermore, even though the ECA is a widely used index in landscape connectivity studies (Keeley et al. 2021), it tends to underestimate connectivity for species with limited dispersal abilities (Marcantonio et al. 2024), further explaining these results. To benefit short dispersal species, FGP should be established in narrow gaps or riparian buffers and complemented with smaller semi-natural features such as hedgerows or isolated trees.

Although we focused on three common forest bird species, many others could also benefit from increased connectivity provided by FGP. In our literature review, we found that different bird species sharing similar dispersal distances as our focal species were reported to occur in poplar plantations (see Table S1). Some of them are listed in Annex I of the European Birds Directive (DIRECTIVE 2009/147), which emphasizes that species of conservation concern can use FGPs as habitats and as steppingstones in between N2000 forests. Including them as focal species helps ensure that connectivity strategies support both biodiversity conservation goals and legal protection requirements.

Differences in modeled functional connectivity were also notable between sub-catchments, suggesting the benefits of FGP on connectivity depend on the landscape context. Only in the Spanish sub-catchment we observed a higher contribution of plantations to connectivity relative to the increase in habitat area they provide (dECA vs. dA*suit), consistently across all scenarios (Table 1). This suggests that although connectivity will always increase when more habitat is added (for the metrics considered), the effectiveness of this measure depends on other landscape characteristics. In our case, these differences between sub-catchments might be related to the spatial configuration of forest habitat patches. In fact, for scenario 4 (all habitat patches), forest patches in Spain were on average much more aggregated than in France, which was reflected in the mean values for the Euclidean nearest-neighbor distance (94.7 vs 193.6 m). This finding resonates with the work of Goodwin and Fahrig (2002) who found that connectivity always declines when interpatch distance increases, and that habitat structure has a more important effect on connectivity than the matrix. Similarly, Marcantonio et al. (2024) showed that spatial arrangement and patch shape influence the degree to which woody habitats enhance connectivity in agricultural landscapes. These findings highlight that efforts to enhance functional connectivity should prioritize the spatial configuration of new woody elements within the existing patch network.

The importance of small patches for connectivity across N2000 sites

Previous studies have highlighted the lack of habitat connectivity among the N2000 protected areas (Estreguil et al. 2013; Opermanis et al. 2013; Rincón et al. 2021), and their dependence on the quality of the surrounding landscape matrix (Orlikowska et al. 2020). This is consistent with our results, where there is a pronounced low connectivity for protected forest patches within both sub-catchments, reflected in the low values of PC% for scenarios 1 and 2 across all species (see Fig. 3). Regarding the importance of individual patches for scenario 2, most plantations fall within the lowest dPC classes, indicating little individual importance for connectivity within the N2000 sites (Fig. 4). In contrast, high-value forest patches were concentrated in a few key regions, suggesting that connectivity relies primarily on localized forest networks rather than the broader distribution of plantations.

Nevertheless, small habitat patches are known to play an important role in agroecosystems (Cadavid-Florez et al. 2020) and biodiversity conservation (Riva and Fahrig 2022), acting as steppingstones that connect larger forest remnants. While FGPs do not provide the same structural complexity or ecological functions as natural forests, our results indicate that they can nonetheless contribute to landscape connectivity. In our study, plantation patches were much smaller on average than natural forest patches (Table 1) and had lower individual dPC values (Fig. 4). However, their effect as steppingstones was notable when considered relative to their area (greater contribution to PC% than as habitat area). In Spain, the addition of just 3% of plantation area (from scenario 1 to scenario 2) resulted in a 14% increase in the total sum of dPCk, indicating an important positive effect on connectivity. In contrast, in the French sub-catchment, a 1% increase in plantation area led to a corresponding 1% increase in dPCk, suggesting a more neutral relationship (only adding habitat area).

To understand the landscape-context factors explaining such differences, we calculated the area of forest habitat patches intersecting a 100 m buffer of the main rivers in both sub-catchments. Spain had 0.34% (7000 ha) of the riverine buffer covered by forests compared to 0.17% (3000 ha) in France. Strips of vegetation along rivers significantly enhance landscape connectivity by serving as ecological corridors and steppingstones, especially in fragmented and human-dominated landscapes (Siqueira et al. 2021). Recent restoration-oriented studies have further highlighted the contribution of small woody linear elements to ecological connectivity between N2000 sites in agricultural matrices (e.g. Valeri et al. 2025), emphasizing their relevance as Green Infrastructure within restoration frameworks. Because plantations in the Spanish sub-catchment are often aligned with linear elements such as rivers, individual patches may enhance connectivity more effectively than in France. However, it is important to emphasize that suboptimal habitats, such as plantations, are not a substitute for natural riparian habitats, which already function as key connecting elements within the N2000 network, particularly in agricultural landscapes (De La Fuente et al. 2018).

Beyond spatial positioning, species-specific traits also strongly influence the contribution of individual patches to connectivity. The ranking of patches based on dPC also varied greatly between species. Values of certain patches in Spain were much higher for the common chaffinch (short dispersal) compared to the Eurasian blackcap (long dispersal) (see Fig. 4 and Figure S2). These high values indicate that, due to the species' limited dispersal capacity, the loss of a single key patch can result in the disconnection of entire local networks, drastically reducing overall functional connectivity for that particular species (Saura and Rubio 2010).

Implications for land use policy and future research

Our study highlights that existing FGP can contribute to enhancing functional connectivity within agricultural landscapes. Plantations alongside natural forests may act as multifunctional landscape elements with the potential to enhance landscape heterogeneity and support conservation objectives in highly human-modified regions (Porro et al. 2020). Current policy frameworks, such as the CAP, could support targeted management of existing plantations to maximize connectivity benefits while remaining consistent with broader restoration and biodiversity goals.

Balancing production and conservation becomes more critical in the context of land use pressures and the expansion of bioenergy and biomass plantations in response to climate change mitigation goals (Popp et al. 2021). As noted by Meller et al. (2015) there might be potential conflicts between biomass expansion and priority areas for conservation. In our study, from the total area of patches, we found around 7000 and 2000 ha of plantations intersecting N2000 sites in Spain and France (see Table 1). While these plantations can play a positive role in enhancing connectivity of protected forest areas in the landscape matrix, it is important to carefully consider their spatial location, avoiding protected sites where long continuity of forest is needed. Furthermore, FGP may also function as barrier for open-habitat species, including waders, and some farmland songbirds such as skylarks (Berg 2002; Zitzmann and Langhof 2023). Therefore, careful consideration is also needed when locating FGP near high-conservation open habitats, such as meadows.

In addition to large-scale planning and policy measures, local biodiversity-friendly management is crucial to maximizing the ecological benefits of plantations for various bird species. Archaux and Martin (2009) highlighted that preserving young plantations can contribute to supporting grassland birds and maintaining understory vegetation in mature poplar plantations, while retaining old or decaying trees, promotes higher bird densities. Additional recommendations, such as alternating biomass plantations with farmland and limiting plot sizes to around 15 hectares, can further support diverse species (Dauber et al. 2010). By increasing the attractiveness of plantations to different kinds of birds, these management practices could play a key role in enhancing biodiversity and strengthening functional connectivity in agroecosystems, while maintaining productive goals.

In fragmented landscapes, forest connectivity can be enhanced by restoring or creating new corridors between existing habitat patches. For example, Dondina et al. (2018) showed that in an Italian agroecosystem, creating new corridors was more effective than restoring existing ones. They also emphasized the importance of hedgerows, which not only support connectivity but also provide habitat for species of conservation concern, such as the Hazel Dormouse. To further enhance connectivity in fragmented landscapes, it is also important to consider both the quality and permeability of the agricultural matrix (Fahrig 2013). Future studies could incorporate resistance surfaces to better model species movement through the landscape and more accurately assess the role of poplar plantations in acting as steppingstones or ecological corridors.

Although plantations typically offer lower habitat quality than natural forests, revised literature suggests that forest species can still use them as steppingstones to move between preferred habitat patches. To reflect this, our analysis incorporated a weighted area approach using species-specific habitat suitability values (see Connectivity Analysis section). However, empirical evidence on the direct effects of FGPs on functional connectivity and their performance as dispersal corridors remains limited, which prevented us from making further comparisons of our results with other studies.

Furthermore, we acknowledge that using natal dispersal as a movement parameter simplifies complex ecological realities. While natal dispersal is a relevant process for inter-patch colonization (Robles et al. 2022), the actual connectivity for our focal species may be higher during rare long-distance or irruptive movements not captured by our model. Therefore, our results should be interpreted as identifying potential connectivity and prioritizing FGP that can enhance connectivity between forest habitat patches.

Finally, while our focus remains on the role of FGP in promoting functional connectivity, they are not the only or optimal tool for enhancing it across the N2000 network. At a national scale, Saura et al. (2018) highlighted that to improve the connectivity of protected areas, Spain and France should also increase matrix permeability (i.e., facilitating species movement through human-dominated or fragmented landscapes) and coordinate the management of adjacent protected areas. As already contemplated in the EU Nature Restoration Regulation, restoring and improving the quality of the matrix in agroecosystems is crucial to enhance connectivity. In this context, some High Nature Value farming strategies, characterized by low-intensity management and the maintenance of heterogeneous semi-natural elements, are associated with high levels of biodiversity and ecosystem service provision across European agricultural landscapes, contributing to landscape heterogeneity and permeability without relying on extensive tree planting (Varela et al. 2025).

While FGPs cannot replace the ecological quality of natural habitats, they can serve as complementary elements to foster biodiversity conservation in certain contexts. Our study highlights the importance of continuing to investigate species-specific responses to biomass plantations to support more informed and effective land-use planning and management decisions.

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Data availability The data supporting our findings are available within the paper and its supplementary material. Should any raw data files be needed, they will be available upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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