

Article

# Effects of Land Use Intensification on Avian Predator Assemblages: A Comparison of Landscapes with Different Histories in Northern Europe

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**Abstract:** Land use and landcover change alter the ability of habitat networks to maintain viable species populations. While their effects on the quality, amount and patterns of landcover patches are commonly studied, how they affect ecological processes, such as predation on focal species remains neglected. This macroecological study tests the hypothesis that predator assemblages are affected by land use intensity linked to different socio-economic contexts. We measured the distribution and abundance of two avian predator groups (generalist corvid birds and specialist raptors), and proxy variables that mirror their food resources, at three spatial scales in northern Europe's West and East. In total, we made 900 survey counts for avian predators and their resources in six landcover strata throughout five landscapes and analyzed their relationships. The abundance of omnivorous corvid birds was associated with the number of anthropogenic food resources. Thus, corvid birds were most common in the urban and agricultural landcovers, and where forest cover was low. Corvid bird abundance, and availability of their resources, increased with increasing land use intensity. Raptors were less abundant than corvid birds and most common in semi-natural grasslands. The number of raptor species increased with decreasing land use intensity. This study shows that the abundance and composition of avian predator species must be understood to maintain functional habitat networks.

**Keywords:** conservation; corvids; ecological processes; ground nesting birds; macroecology; predation; raptors; spatial scale; trophic interactions

## 1. Introduction

To meet increasing societal demands, land use linked to the production of renewable natural resources (e.g., food, feed, fiber and fuel) continues to be intensified [1,2]. With its long land use history, the European continent is a good example of negative consequences for the composition, structure and function of ecosystems, i.e. natural capital [3,4]. Solutions on how to maintain functional networks of habitats have been subject to research, policy and practice in Europe for decades [5,6]. The European Union's green infrastructure (GI) policy appeared in response to the need to communicate the importance of maintaining ecosystems as natural capital [7]. Thus, GI policy in Europe is of paramount importance to conserve and restore habitat networks for both biodiversity and human well-being. According to European Union policy, GI is "a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services" ... "in both rural and urban settings". A key tool towards securing GI is to establish effectively

and equitably managed, ecologically representative, and well-connected systems of protected areas that form functional habitat networks, and that areas under agriculture, aquaculture and forestry are managed sustainably, ensuring the conservation of biodiversity (e.g., Convention on Biological Diversity [8] Aichi targets #7 and #11). This requires assessment as to whether representative landcover types with sufficient patch quality, size, and connectivity, are present [9–11]. The focus is thus on landscape pattern of both natural and semi-natural landcovers [12].

However, intensified land management has also altered ecological processes, such as trophic interactions involving large herbivores and vegetation, and the cascading effects in the boreal forest [13, 14]. Trophic interactions among predators and prey is another example that needs to be considered when analyzing the functionality of habitat networks for biodiversity conservation [15]. Therefore, both landcover patterns (e.g., Reference [16]) and ecological processes [17] need to be understood for planning and management of landcovers and their natural resources towards maintaining functional habitat networks.

Bird assemblages are often used as an indicator to assess the states and trends of biodiversity at multiple spatial scales [18,19]. The abundance and breeding success of birds are dependent on both the patterns of their biophysical landcover patches (e.g., Reference [19]) and the processes within the surrounding landscape's matrix [20,21]. Declines in both semi-natural grassland birds (such as waders (*Charadrii*)) (e.g., References [22,23]) and forest ground nesting birds (such as grouse (*Tetraoninae*) (e.g., References [24–26]), partridges and pheasants (*Phasianinae*) (e.g., References [27,28])) have occurred throughout much of Northern Europe. These declines have been linked to the intensification of land management, which has led to changes in both landcover patterns (e.g., conversion of semi-natural grasslands into arable crops or the intensification of forestry) [16,29] and ecological processes (e.g., hydrological drainage, increased predation) [15,30,31].

Studies on the effects of pattern and process affecting habitat network functionality require both large spatial extents, and study areas that mirror different levels of land use intensification. However, the implementation of land management policies and management strategies within a country often have similar outcomes among landscapes, which result in limited variation in land use and landcovers, and thus limited variation in habitat network functionality [13,14]. For this reason, including multiple study areas with different land management histories can be used to test hypotheses about species-habitat relationships (e.g., References [32,33]). This calls for a macroecological approach (e.g., Reference [34]), i.e. one that considers the importance of using multiple landscapes as case studies in regional socio-economic gradients to explore mechanisms that affect opportunities for biodiversity conservation (e.g., Reference [35]).

Western Europe is a prime example of a region with a long history of land management developed to meet the increasing demands for goods of a market economy [36]. This economic driver has simultaneously placed unwanted strain on natural and semi-natural ecosystems [37], as well as on traditional land management systems in agricultural landscapes [29]. This has caused difficulties for the implementation of biodiversity conservation policies [38]. Intensification of land management in Western Europe is thus responsible for declines and even local extinction of species [30]. In comparison, land management and use in Eastern Europe has developed slower, and is generally less intensive [3,36,39,40]. Despite the expansions to large scale farming during the Soviet era, traditional land management activities are still practiced locally [41,42]. The different landscape histories throughout the European continent have led to different ecological, economic and socio-cultural states. As a result, a range of species that are no longer found in Western Europe remains in Eastern Europe [19,30,32,43,44]. This circumstance can be used to define reference benchmarks for landscape restoration in Western Europe [45] and forms an important complement to historical ecology studies [29]. Therefore, the regional diversity of landscapes and regions on the European continent provides unique opportunities to develop evidence-based knowledge for biodiversity conservation. This can be achieved by designing replicated studies on relationships between landscape patterns and processes on the one hand, and their effect on the functionality of habitat networks as GI on the other.

The aim of this study is to test the hypothesis that the level of anthropogenic land use intensification at different spatial scales explain the distribution and abundance of two avian predator groups with different resource requirements, viz. omnivorous generalist corvid birds (*Corvidae*) and carnivorous specialized raptors (*Accipitriformes*). We tested the predictions that (1) the abundance of corvid avian predators should be higher in landscapes and landcover patches located in regions with higher anthropogenic resource diversity and abundance, and (2) that the abundance of raptors should be higher in landscapes and landcovers patches in regions with lower land use intensification.

## 2. Materials and Methods

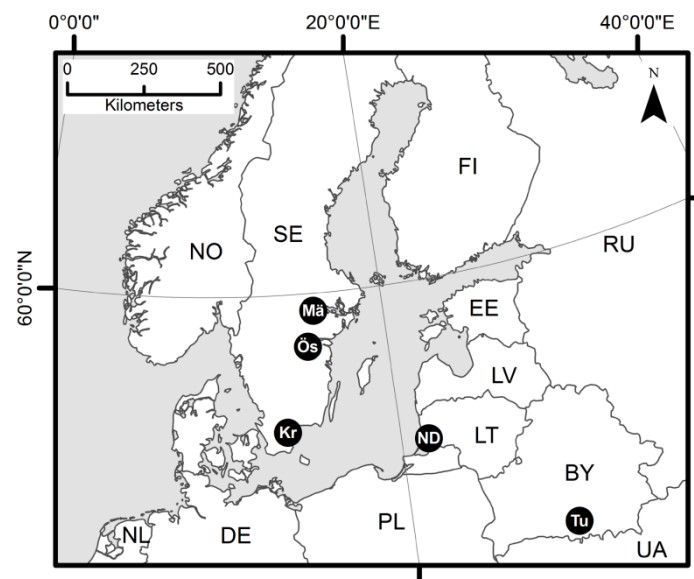
### 2.1. A Macroecological Approach Based on Multiple Landscapes

The scale dependency of species-habitat relationships (e.g., References [46,47]) highlights the need to include at least three spatial scales: (1) Points within local landcovers [48], (2) patterns and processes at the spatial scale of focal species' landcover patches within a landscape [49], and (3) at coarser scales, such as landscapes in different regions [50]. A macroecological approach [34] satisfies this need to include the trade-off between the precision of small-scale research in patches of habitat [51], the spatial scale of the local landscape as a social-ecological system [52], as well as different regional contexts linked to different landscape histories affecting land use intensification [3,53].

### 2.2. Three Spatial Scales

#### 2.2.1. Landscapes with Different Land Management

The European continent's West and East provides appropriate gradients in both land use intensity [45,54], and the states and trends of bird populations (e.g., References [19,55]). This is particularly pronounced in the Baltic Sea Region hosting countries with different trajectories of land use intensification in the West and the East, respectively [37,56]. Case study research is a strategy that focuses on understanding a given context [57] and is an essential method to understand the dynamics within both singular and multiple settings [58]. We selected five case study landscapes in the Baltic Sea Region' West and East with different landscape histories and levels of land use intensification in the temperate-hemi-boreal ecoregions in Southern Sweden, Lithuania and Belarus (Figure 1, Table 1).



**Figure 1.** Locations of the five case study landscapes in Sweden (SE) (Kristianstad (Kr), Östergötland (Ös), Mälardalen (Mä)), in Lithuania (LT) (Nemunas Delta (ND)) and in Belarus (BY) (Turov (Tu)).

Southern Sweden in the West has a very long land management history (e.g., Reference [59]) that has favored maximum sustained yield production in agriculture and forestry [60,61]. The three Swedish case study landscapes chosen are dominated by intensively managed arable fields managed for feed and food, and forests managed for fiber and biomass production. Historically, under traditional low-intensity land use systems, these landscapes hosted greater abundances of ground nesting birds of conservation concern compared to today [15,62]. First, the Kristianstad landscape (1370 km<sup>2</sup>) is one of Sweden's most important agricultural production areas [63]. In addition, this landscape contains the acclaimed Kristianstad Vattenrike (Water Kingdom in Swedish) Biosphere Reserve, established in 2005 to support ecological, economic and social systems for sustainable development [64]. Second, the Östergötland landscape (2146 km<sup>2</sup>) in central southern Sweden is home to both intensive agricultural production and forest management. Third, the Mälardalen landscape (2028 km<sup>2</sup>) in south-central Sweden is characterized by a transition of agricultural fields in the south to predominantly forest in the north. The landscape mosaics are fine-grained with many land owners.

In contrast, Lithuania still hosts traditional farming and less intensive forestry practices, both being beneficial for biodiversity conservation [65,66]. During the past century Lithuania has experienced many major political shifts, including to and from Soviet occupation, independence, achieving a market economy, and EU membership. All previously privately owned agricultural and forest land became state-owned under Soviet occupation (1945–1990). Since re-gaining independence (1990), land restitution back to private owners has been implemented. We selected the Nemunas river delta as the case study landscape (1318 km<sup>2</sup>). This area is a regional hotspot for bird conservation in Lithuania [67,68]. The landscape is farmed predominantly for dairy produce and fodder for livestock. However, since regaining independence the Nemunas river delta landscape has experienced both elevated levels of land abandonment, and more recently intensification of the forest and agricultural sectors.

Belarus further to the East has a planned economy and has undergone its own transitions leading to state ownership of forest and agricultural land, and with large landcover patches. Indeed, past legacies from the Soviet period can still be found within the rigid land management and use policies still enforced [65]. For instance, the Belarussian government still stipulates the type and quantity of crops to be grown by co-operative farming units [69]. Based on the landscape history of Belarus, we selected the Turov landscape (1349 km<sup>2</sup>) situated within the mid Pripjat River Valley as a case study. The Turov landscape still retains patterns and processes characteristic of both natural and traditional cultural landscapes [70]. As a result, this landscape also contains large protected areas containing important forest and agricultural habitats for ground nesting birds [71,72].

This spectrum of landscape histories across the five case study landscapes forms a macroecological gradient in land use and landcover change, which can be used to understand factors that affect the abundance of the chosen two groups of avian predators (corvids and raptors). Moreover, this selection of landscapes ensures that a large variation in the conservation status (from unfavorable in the West to favorable in the East) of habitats for ground nesting birds is covered. This can help define benchmarks for the restoration of ecological processes affecting the functionality of habitat networks in the same way as historical ecology research [29].

### 2.2.2. Stratification of Landcovers

The six dominant landcover strata across the five case study landscapes, all of which with forest as the natural potential vegetation, were (1) urban area (URB), (2) agricultural land (AGR) (forest cover <5%), (3) semi-natural grassland (GRASS), (4) low forest cover (LOWF) (5–20%), (5) mixed forest and agricultural land (MIXF) (forest cover 40–60%) and (6) high forest cover (HIGHF) (80–95%) (Table 1). The forest cover intervals were chosen to include areas with different landcover proportions. The rationale for this stratification is that the spatial patterning of resources limits the movement of species within a landscape, as well as affects ecological processes (e.g., References [48,73]). This is captured by percolation theory which predicts that species can freely move between patches of suitable

habitat if the focal species' habitat meets a threshold of >40–50% [74], and by critical thresholds for habitat loss of ca. 20% (e.g., Reference [75]).

**Table 1.** Description of the five landscape case studies in the Baltic Sea Region's West-East gradient (see Figure 1).

Case Study Landscape from West to East	Sweden			Lithuania	Belarus
	Kristianstad	Östergötland	Mälardalen	Nemunas Delta	Turov
Latitude	55°59' N	58°25' N	59°50' N	55°18' N	52°4' N
Longitude	14°12' E	15°35' E	16°20' E	21°20' E	27°44' E
Area km <sup>2</sup>	1370	2146	2028	1318	1349
Biogeographical region	Temperate	Hemiboreal	Hemiboreal	Hemiboreal	Temperate
Population density (n/km <sup>2</sup> )	45	40	39	30	16
Population change 1965–2015	1.40	1.22	1.07	0.74	0.58
GDP per capita	37648	39000	37492	30501	18804
<b>Dominating focal and other landcovers (%)</b>					
Urban areas (URB)	4.3	2.5	2.2	0.3	0.5
Agricultural land (AGR)	34.3	28.6	26.0	33.9	16.9
Semi-natural grassland (GRASS)	1.3	0.5	1.0	31.7	37.1
Low forest (LOWF)	15.7	21.9	18.2	7.7	14.2
Mixed forest (MIXF)	11.5	13.6	14.1	7.0	7.2
High forest (HIGHF)	6.7	15.4	15.2	4.5	5.8
Other	32.9	17.5	23.3	14.9	18.3
<b>Total</b>	100	100	100	100	100

To map the amount of the six focal landcover types (Table 1) we used a Geographical Information System [76] to create a 1-km<sup>2</sup> grid covering the five case study landscapes [15]. Each grid cell was attributed to one of the six focal landcover strata. Any cell within the case study landscapes that did not fall into our landcover design classification (e.g., one of the six dominant landcovers) were omitted from the field study of predators and their resources. As we only focused on the representativeness of landcover proportions within each 1-km<sup>2</sup> cell, we selected matching combinations of landcover data. We used the European CORINE landcover data (2012) for the Swedish and Lithuanian case study landscapes within the European Union [77]. This included the following classifications; Urban areas level 2 codes 1.1, 1.2, 1.3 and 1.4, Agricultural land level 2 codes 2.1, 2.2, and 2.4, Forest cover level 2 code 3.1 and for semi-natural grasslands we used level 2 codes 2.3, 3.2 and 4.1. As the European CORINE landcover data (2012) did not include Belarus, we used the GlobCover 2009 landcover data [78] to define urban areas (code 190), agricultural land (level 1 codes 1–32) and semi-natural grasslands (level 1 codes, 140–143) and forest (level 1 codes 40–120). Because semi-natural grassland status is affected by conservation management and can change rapidly, even from one year to the next, we validated the GRASS strata with the help of local experts. This was done using their cartographic data with the same spatial resolution as the CORINE landcover data. The semi-natural grassland mapping with local land managers was given priority over the landcover data derived from the databases.

### 2.2.3. Avian Predator Counts

To estimate the variation in abundance of the two groups of avian predators in the different landcovers we used the same 1-km<sup>2</sup> landcover stratification grid to randomly select from each of the five case study areas, and each of the six landcover strata, a total of 30 1-km<sup>2</sup> grid cells amounting to a grand total of 900 (5 × 6 × 30) survey points. The 1-km<sup>2</sup> grid cell area represents the local patch scale and matches the minimum area requirements of breeding ground nesting birds [19,29,79]. During the latter part of the breeding period of both ground-nesting grassland and forest birds, in early June of 2013–2015, we counted corvids (generalist omnivores) and raptors (specialist carnivores) once in each of the five case study landscapes. We focused on six common omnivorous corvid bird species known for preying on the eggs and young of ground nesting birds, as well as all raptors that are known to prey on young and adult ground nesting birds (Table 2). At the center of each randomly selected 1-km<sup>2</sup>

grid cell a 20-min, continuous 360° point sweep with binoculars was undertaken to count corvids and raptors. A maximum visual distance of 500 m was applied so observations were not taken beyond the borders of the 1-km<sup>2</sup> cell. To minimize the difference between the visibility of urban, agricultural and grasslands on the one hand, and area with forest cover on the other, we located clear cuts, young forests and high vantage points within the 1-km<sup>2</sup> cell to undertake the counts. The point counts were suspended in adverse weather conditions, such as when windy and rainy.

### 2.3. Proxy Data for the Local Diversity of Food for Predators

Human activities affect landcovers and thus the distribution and abundance of habitat patches, and therefore the local amount of resources. Urbanization and other forms of anthropogenic modification of ecosystems can improve the conditions for species that can adapt to human conditions. Omnivorous corvid birds have benefited from anthropogenic modification through their general ability to utilize a diversity of food resources [80–82]. To estimate the resource density linked to the anthropogenic intensification of land use we counted the number of active farms and livestock manure piles, and the number and type of livestock, within the same randomly selected 1-km<sup>2</sup> landcover stratification grid within the six different landcover strata (900 points in total) (Table 2; Table 3). In contrast, carnivorous raptors are more likely to be constrained to patches with a high abundance of wild prey, such as birds, small mammals and large insects [83,84]. To capture the resource availability for raptors we used the six landcover strata defined above. We ranked them from the highest in semi-natural grassland and open agriculture landcovers and the decreasing with increasing forest cover, and urban as the least important landcover for raptors.

### 2.4. Statistical Analyses

To explain the variation in the abundances of corvid birds and raptors we employed mixed-effects generalized linear models with a Poisson link function for the non-negative discrete response variable (counts of birds) fitted by Laplace approximation [85] using the statistical software R [86] with the lme4 package [87]. Positive integer explanatory variables were square-root-transformed to satisfy the constant variance assumption of a linear modelling. To account for over dispersion, we used individual-level random effects method Poisson simulation with single covariate which is uniformly and randomly distributed [88]. We started with a saturated model containing all variables and selected explanatory variables by backward elimination with significance level  $p < 0.05$ . The resulting models for corvids and raptors had the lowest Akaike information criterion (AIC) compared to all other possible combinations of variables. The significance of the regression parameters in the different models was estimated pairwise by analysis of deviance (Pearson's Chi-square test). Based on the significant results of mixed-effects generalized linear models (Table 4) we also ran a multivariate analysis to visualize the different effects of the landscapes variables on the two avian predator groups. We did this by using (I) a principle component analysis (PCA) on the five case study landscapes areas, observations of corvid birds and resource availability using data from Tables 2 and 3; and (II) we ran a PCA on the landcover strata and raptors.

**Table 2.** Number of observed omnivorous corvid birds and carnivorous raptors observed during this study, and their dietary requirements [82,83].

	Species	Case Study Landscape					Diets
		Kr	Ös	Mä	ND	Tu	
Corvids	Magpie ( <i>Pica pica</i> )	122	76	67	32	58	Invertebrates, fruits, seeds, carrion, scraps, refuse, small vertebrates and bird eggs
	Jay ( <i>Garrulus glandarius</i> )	9	8	9	18	4	
	Jackdaw ( <i>Corvus monedula</i> )	908	572	1408	59	10	
	Rook ( <i>Corvus frugilegus</i> )	435	0	27	239	942	
	Hooded Crow ( <i>Corvus cornix</i> )	377	149	147	80	130	
	Raven ( <i>Corvus corax</i> )	23	16	18	35	60	
	<b>Total number of corvids</b>	<b>1874</b>	<b>821</b>	<b>1676</b>	<b>463</b>	<b>1204</b>	
Raptors	White-tailed Eagle ( <i>Haliaeetus albicilla</i> )	0	1	5	14	5	Fish, birds, mammals and carrion
	Lessor Spotted Eagle ( <i>Aquila pomarina</i> )	0	0	0	3	3	Small mammals, birds, amphibians, and reptiles
	Short Toed Eagle ( <i>Circaetus gallicus</i> )	0	0	0	0	2	Reptiles, small birds, invertebrates
	Red Kite ( <i>Milvus milvus</i> )	33	0	1	0	0	Small mammals, birds, reptiles, amphibians, fish and invertebrates
	Black Kite ( <i>Milvus migrans</i> )	0	0	0	1	0	
	Marsh Harrier ( <i>Circus aeruginosus</i> )	14	10	19	14	38	Small mammals, birds, reptiles, amphibians and invertebrates
	Montagu's Harrier ( <i>Circus pygargus</i> )	0	0	0	0	2	
	Buzzard ( <i>Buteo buteo</i> )	20	5	13	7	8	Birds and small mammals
	Hen Harrier ( <i>Circus cyaneus</i> )	0	0	0	2	2	
	Sparrowhawk ( <i>Accipiter nisus</i> )	0	0	0	0	1	Small birds
	Kestrel ( <i>Falco tinnunculus</i> )	0	1	6	0	7	Small mammals, birds, invertebrates and reptiles
	Hobby ( <i>Falco subbuteo</i> )	3	1	4	0	2	Small birds and insects
	Peregrine Falcon ( <i>Falco peregrinus</i> )	0	0	0	0	1	Birds
<b>Total number of raptors</b>	<b>70</b>	<b>18</b>	<b>48</b>	<b>41</b>	<b>71</b>		

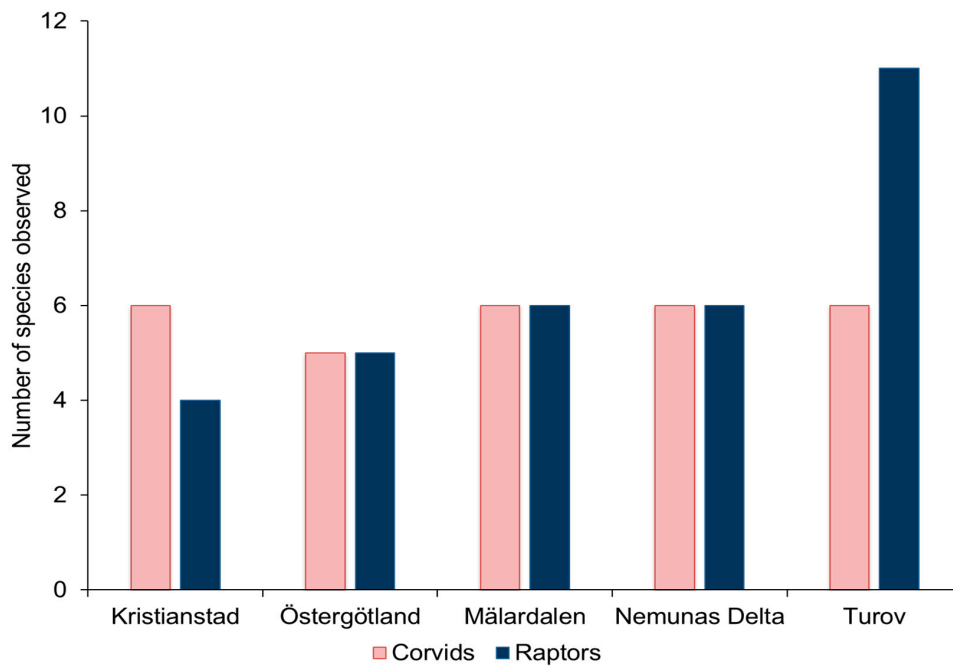
Kr = Kristianstad, Ös = Östergötland, Mä = Mälardalen, all in Sweden, ND = Nemunas Delta, Lithuania and Tu = Turov, Belarus.

### 3. Results

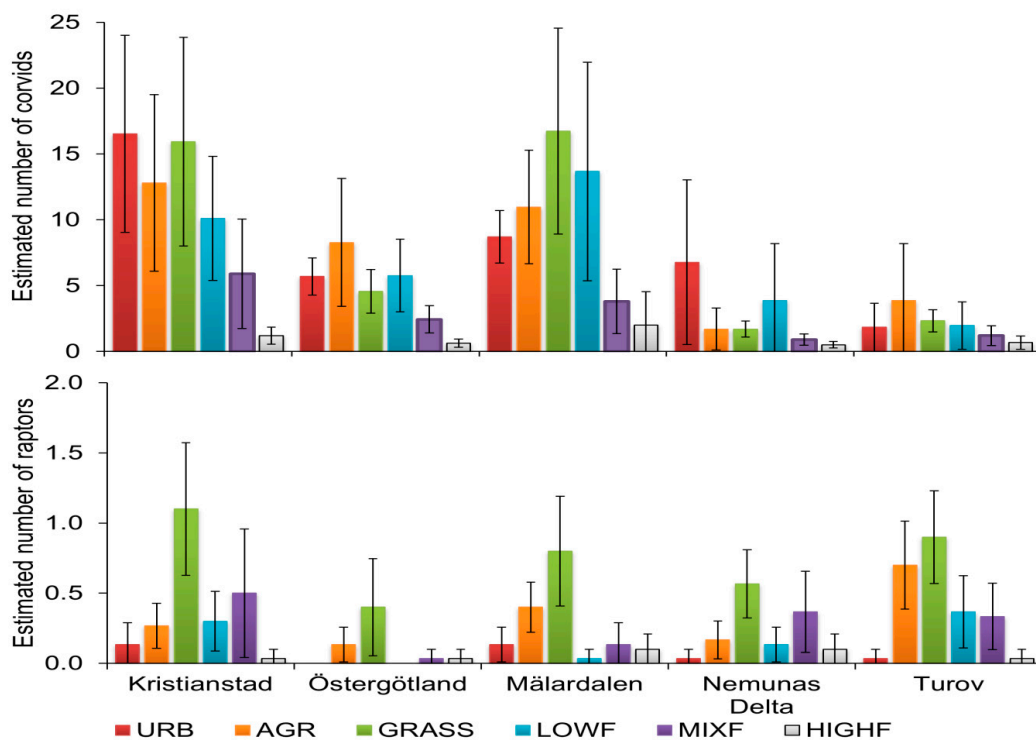
#### 3.1. Avian Predators in Different Landscapes

At the macroecological level the number of omnivorous corvid species was similar throughout the five case study landscapes with 5–6 species observed (Figure 2). However, the number of corvid birds varied much among the five case study landscapes. The abundance of corvid birds was highest in the Swedish case study landscapes with jackdaw and hooded crow the dominant species (Figure 3, Table 2). The Kristianstad and Mälardalen landscapes recorded the largest numbers of corvid bird observations per point with a mean of 10.41 and 9.31 individuals, respectively (Table 3). The abundance of corvids was lowest in the Nemunas Delta and Turov with 2.57 and 1.97, respectively (Figure 3, Table 3). There was a significant difference (Chi-test = 190, df = 4,  $p < 2.2 \times 10^{-16}$ ) among the abundances of corvid birds in the five landscapes (Figure 3, Table 4). Thus, the prediction that anthropogenic land use intensification explains the distribution and abundance of corvid bird predators cannot be rejected.

In contrast, raptors were observed at much lower numbers than corvid birds across the five case study landscapes. The number of raptor species varied from four species in Kristianstad to 11 in Turov (Figure 2). The number of raptors varied significantly among landscapes (Table 4, Chi-test = 25.6, df = 4,  $p < 3.8 \times 10^{-5}$ ), and the mean number of raptors per observation point ranged from 0.1 in Östergötland to 0.39 in Turov (Table 3).



**Figure 2.** The number of corvid and raptor species observed in the five case study landscapes in the Baltic Sea Region.



**Figure 3.** Mean number of corvid (top) and raptor (bottom) observations per point with 95% confidence intervals among the 6 landscape strata; urban area (URB), agricultural land (AGR) (forest cover <5%), semi-natural grassland (GRASS), low forest (LOWF) (cover 5–20%), mixed forest and agricultural land (MIXF) (forest cover 40–60%) and high forest cover (HIGHF) (80–95%) in the five case study landscapes in Sweden (Kristianstad, Östergötland and Mälardalen), Lithuania (Nemunas Delta) and Belarus (Turov).



**Table 3.** Mean number of observations with standard error ( $\pm$ ) of dependent and independent variables at the point scale level (i.e., at each 1-km<sup>2</sup> cell) within the five case study landscapes in the Baltic Sea Region.

		Case Study Landscapes from West to East				
		Sweden			Lithuania	Belarus
Type of variable		Kristianstad	Östergötland	Mälardalen	Nemunas Delta	Turov
Dependent	Corvid birds	10.41 $\pm$ 1.25	4.56 $\pm$ 0.54	9.31 $\pm$ 1.14	2.57 $\pm$ 0.67	1.97 $\pm$ 0.43
	Raptors	0.38 $\pm$ 0.06	0.1 $\pm$ 0.03	0.26 $\pm$ 0.04	0.22 $\pm$ 0.39	0.39 $\pm$ 0.05
Independent	Livestock	6.26 $\pm$ 1.08	3.74 $\pm$ 0.84	4.46 $\pm$ 0.81	10.30 $\pm$ 1.31	8.01 $\pm$ 2.95
	Horses	0.63 $\pm$ 0.11	0.58 $\pm$ 0.16	0.46 $\pm$ 0.12	0.22 $\pm$ 0.06	0.26 $\pm$ 0.05
	Cows	4.29 $\pm$ 0.93	3.04 $\pm$ 0.83	3.67 $\pm$ 0.77	10.07 $\pm$ 1.30	7.64 $\pm$ 2.95
	Sheep	0.92 $\pm$ 0.37	0.13 $\pm$ 0.09	0.33 $\pm$ 0.21	0.01 $\pm$ 0.01	0.08 $\pm$ 0.08
	Farms	0.89 $\pm$ 0.09	0.97 $\pm$ 0.08	0.60 $\pm$ 0.06	0.78 $\pm$ 0.09	0.12 $\pm$ 0.03
	Manure	0.18 $\pm$ 0.04	0.07 $\pm$ 0.02	0.19 $\pm$ 0.04	0.28 $\pm$ 0.05	0.12 $\pm$ 0.03
	Recreational areas	0.27 $\pm$ 0.03	0.26 $\pm$ 0.03	0.17 $\pm$ 0.03	0.10 $\pm$ 0.02	0.02 $\pm$ 0.01

### 3.2. Avian Predators in Different Landcover Strata

At the landcover strata scale, the abundance of corvid birds was significantly different among the five case study landscapes (Chi-test = 163, df = 5,  $p < 2.2 \times 10^{-16}$ ) (Table 4). In both the Nemunas Delta and Turov landscapes all strata, except the high forest stratum with 80–95% cover (HIGHF), showed exceptionally low values compared to the three Swedish landscapes. Generally, the urban stratum (URB) had the highest abundance of corvid birds in the West. This was typically followed by the semi-natural grassland strata (GRASS). The high forest cover stratum (HIGHF) showed the lowest number of observations of corvid birds (Figure 3). In contrast, raptors were most abundant in the semi-natural grasslands (GRASS), followed by the agricultural (AGR) and forest-field (LOWF) strata. Östergötland showed the same trend in each stratum as the other four case study landscapes, but with a lower abundance of raptors.

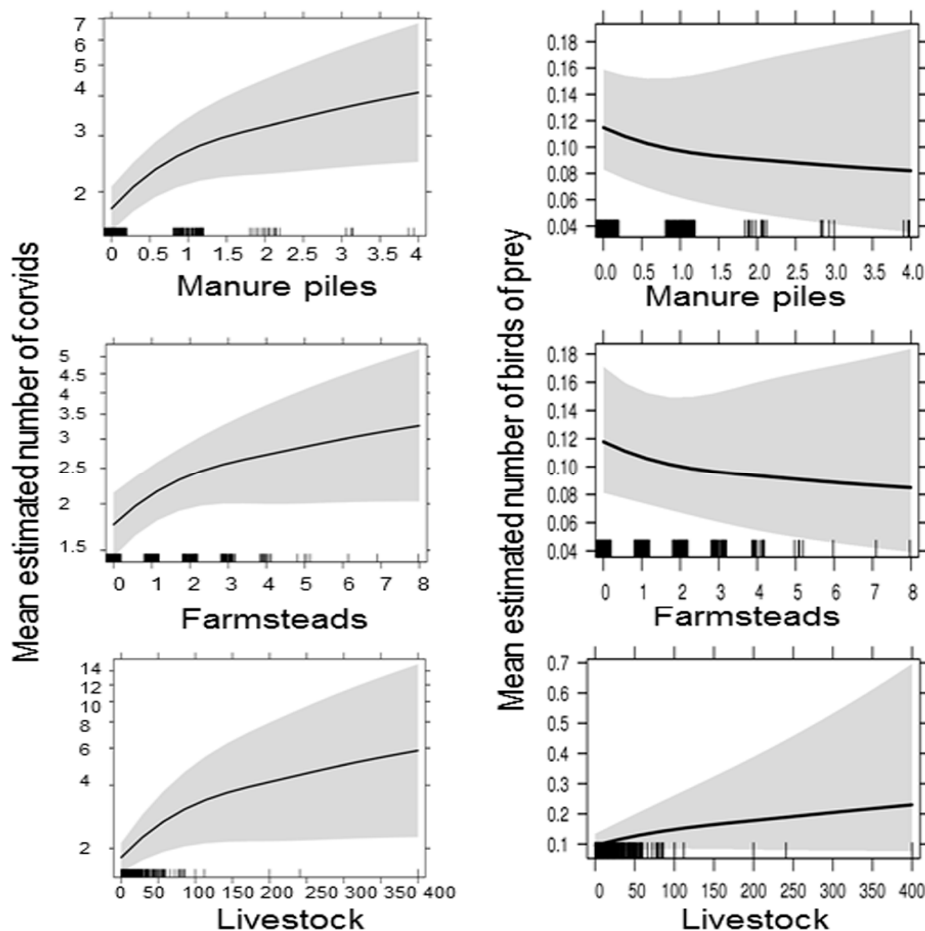
### 3.3. Avian Predators and Local Resource Abundance

At the point scale, linked to the 1-km<sup>2</sup> grid cells, the results from the generalized linear mixed model showed that the corvid bird species were significantly related to manure piles (Chi-test = 8.3, df = 1,  $p = 0.004$ ), farms (Chi-test = 4.1, df = 1,  $p = 0.044$ ), and total number of livestock (Chi-test = 8.3, df = 1,  $p = 0.025$ ) (Table 4, Figure 4). Further analysis of livestock showed that horses and cows were significantly related to higher abundances of corvids (Chi-test = 3.9, df = 1,  $p = 0.046$ ). We found no relationship between corvids and sheep. In contrast, raptors showed no correlation with any of these anthropogenic factors at the point scale level (Table 4, Figure 4).

**Table 4.** Significance tests for regression parameters in the corvids and raptor avian predator models.

Regressor	Corvids			Raptors		
	Chi-Square Test	Df	<i>p</i> -Value	Chi-Square Test	Df	<i>p</i> -Value
Landscape	189.5	4	$<2.2 \times 10^{-16}$ ***	25.6	4	$3.8 \times 10^{-5}$ ***
Landcover strata	163.1	5	$<2.2 \times 10^{-16}$ ***	82.6	5	$2.3 \times 10^{-16}$ ***
Landscape and landcover strata	36.1	20	0.015 *	−1.84	20	0.091
Manure (sqrt)	8.3	1	0.004 **	−0.08	1	0.649
Farms (sqrt)	4.1	1	0.044 *	−0.07	1	0.596
Total Stock (sqrt)	5.1	1	0.025 *	0.04	1	0.127
Horses	3.9	1	0.046 *	−	−	−
Cows	4.1	1	0.044 *	−	−	−

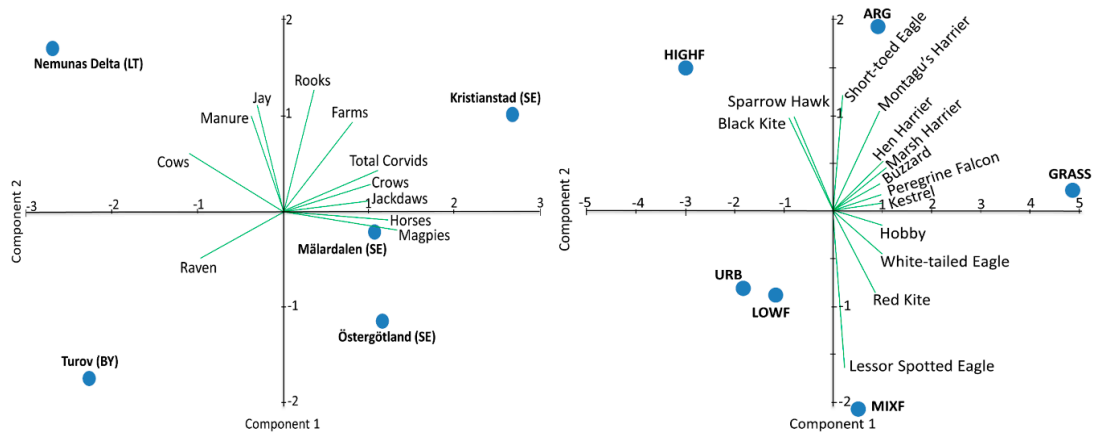
$p < 0.05$  \*,  $p < 0.01$  \*\*,  $p < 0.001$  \*\*\*, − not significant.



**Figure 4.** The mixed-effects generalized linear model predictions for corvid birds (left) and raptors (right) and their relationships with three proxy variables of resource density in terms of manure piles (top), farmsteads (middle) and livestock (bottom). The black line indicates the mean predicted value, the shaded areas represent 95% confidence intervals and the black tick on the horizontal axis are the raw data. Note that for raptors, none of the relationships were significant.

The PCA on corvid birds and resource availability among the five case study landscapes showed that axes 1 and 2 explained 75% of the variation in the dataset. The variables raven, jay, cows and manure piles were all related to negative values of PC1. On the other hand, jackdaw, crow and magpie, and horses and farms were related to positive values of PC1 (Figure 5, Table 5). Rook was intermediate between the jay and the magpie, jackdaw and hooded crow group. Based on the four identified groupings from the PCA (1) raven, (2) jay, (3) rook and (4) the combination of magpie, jackdaw and hooded crow, we compared the metabolic weights (see References [82,83,89]) of each corvid species, including the combination of group 4, and multiplied them by the number of observations to create a proxy of energy requirements at the landscape scale (Figure 6). In Sweden, this predation pressure index (see Reference [15]) was clearly higher for the combination group of magpie, jackdaw and hooded crow compared to the other corvid bird species and the two landscapes in Lithuania and Belarus. Thus, there was a clear gradient in resource availability for the three species (magpie, jackdaw and hooded crow) most closely linked to anthropogenic resources provided by horses and farms. This matches the rank of landscapes in terms of human population density, change in human population and GDP per capita (Table 1).

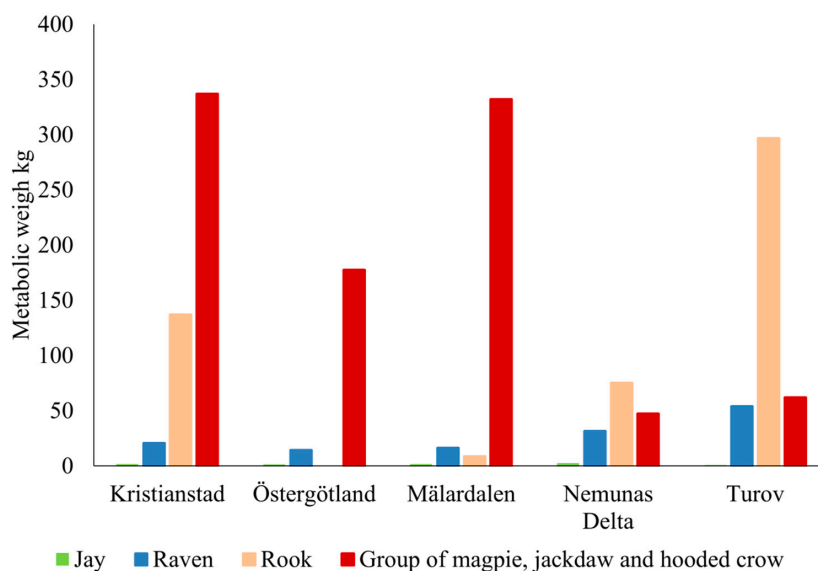
The PCA on landcover by raptor species indicated that axes 1 and 2 explained 77% of the variation in the data set. The results show that raptors were most abundant in the semi-natural grassland and the open agricultural landcovers (Figure 5, Table 5).



**Figure 5.** PCAs of 5 case study landscapes by corvid birds and resources availability (left) and landcover strata by raptor species (right). The landcover strata correspond as: Urban area (URB), agricultural land (AG) (forest cover <5%), semi-natural grassland, (GRASS) sparse forest (LOWF) (cover 5–20%), mixed forest and agricultural land (MIXF) (forest cover 40–60%) and high forest cover (HIGHF) (80–95%).

**Table 5.** Left side of the table shows the loadings for the principal components 1 and 2 of the 5 case study landscape variables and corvids (Figure 5, Table 2; Table 3). Right side of the table shows the loadings for principal components 1 and 2 of the landcover strata variables and raptors (Figure 5).

Corvids	PCA 1	PCA 2	Raptors	PC 1	PC 2
Jackdaw	0.80	0.02	White-tailed Eagle	0.31	−0.12
Crow	0.79	0.16	Lesser Spotted Eagle	0.06	−0.60
Raven	−0.76	−0.28	Short-toed Eagle	0.04	0.41
Rook	0.24	0.67	Red Kite	0.32	−0.26
Magpie	0.89	−0.07	Black Kite	−0.19	0.31
Jay	−0.27	0.90	Marsh Harrier	0.35	0.16
Horses	0.97	−0.09	Hen Harrier	0.34	0.19
Cows	−0.88	0.41	Montagu’s Harrier	0.28	0.36
Manure	−0.31	0.86	Buzzard	0.32	0.09
Farms	0.24	0.33	Sparrowhawk	−0.19	0.31
Corvids Total	0.58	0.53	Kestrel	0.32	0.03
			Hobby	0.31	−0.06
			Peregrine Falcon	0.32	0.05



**Figure 6.** Landscape scale proxy of energy requirements for the four identified corvid bird groupings based on the PCA results for corvid bird species abundance and resources availability (Figure 5).

## 4. Discussion

### 4.1. Omnivorous Corvid Birds and Carnivorous Raptors

The overall abundance of omnivorous corvid birds was higher in Sweden with more intense land use representing Europe's West compared to the case study landscapes in Lithuania and Belarus, both located in Europe's East. The higher abundance of corvid birds at the landscape scale was linked to higher resource availability in their preferred landcovers. This is consistent with the differences in the level of economic development as a proxy of land use intensification in the three countries ([36,90]; see also Table 1). The assemblages of raptor species differed among the landscapes with the Swedish landscapes hosting fewer species. These differences can be attributed to the level of anthropogenic modification compared to the natural dynamics of the selected landscapes [91]. In Sweden, the diversity and abundance of raptors has slowly recovered after many species faced local extinctions during the 1970s [92]. This is linked to changes in land use policy and raptor rehabilitation programs [92]. We identified two species that have increased due to policy changes and programs. Firstly, the red kite population in the Kristianstad landscape portrays the success of the policy changes, rehabilitation and winter-feeding programs. Secondly, the Nemunas delta has experienced its own success with the white-tailed eagle population increasing from near extinction at the end of the 1980s. This can be attributed to less intensive chemical use in farming and change in hunting policies in Europe. In contrast, the species composition and abundance of raptors has remained constant over the past century in Belarus [93]. Nevertheless, as our results show, there are still difference between the species assemblages of raptors in Europe's East and West.

At the landcover strata scale, corvid birds were most abundant in the urban strata followed by the semi-natural grasslands, and their abundance decreased as the forest cover increased. This was linked to the higher resource availability associated with human land use management, which is consistent with the association of omnivorous corvid bird to anthropogenic resources [80,94,95]. However, raptors showed a different pattern compared to the corvid birds. Raptors were most abundant in the semi-natural grassland strata in all case study landscapes, their abundance decreased as the amount of forest cover increased, and they avoided the urban stratum. As predicted by the gradient from semi-natural grasslands to urban, this is linked to prey availability affecting the distribution and abundance of the predator species [96–98]. Indeed, the aquatic-terrestrial ecotone within the semi-natural grassland stratum is generally the most species rich landcover [99–103]. Thus, we agree with Panzacchi, et al. [104] that the higher abundance of raptors in the semi-natural grasslands is because this habitat supports higher abundances of their prey.

At the local point scale of 1-km<sup>2</sup> grid cells, factors related to resource diversity and availability, i.e., farms, piles of manure and abundance of livestock, were significantly related to the corvid birds (magpie, jackdaw and hooded crow). The results revealed that different species of domestic livestock had different relationships to different species of corvid birds; there was a positive relationship between corvid birds and cows and horses, respectively. Although our study did not find any relationship between corvid birds and sheep, previous studies have found the distribution of raven was historically related to sheep farming [105,106]. However, in the five case study landscapes large scale sheep farming does not occur. In Sweden, the number of horses has increased from 88,600 horses in 2000 to 362,700 in 2010, whilst the number of most other farm animals has declined [107]. The use of horses has transformed from a traditional work purpose on a low nutrient diet, to cherished pets for recreation use fed with high nutrient diets (e.g., Reference [108]), and consequently highly nutrient-rich manure. Research by Parvage [109] on nutrient excretion of Swedish horse manure, indicated that horses can add up to 60 kg of phosphorous/y/ha, which is nearly triple the amount farmers are legally permitted to apply to their fields and crops. Simultaneously, most corvid species have increased in abundance in southern Sweden over the past few decades [92]. In contrast, we did not find any relationship between the anthropogenic factors and raptors.

#### 4.2. Multi-Scale Management of Patterns and Processes Affecting Habitat Networks

The macroecological approach used in this study demonstrates the importance of studying multiple spatial scales to understand the differences in avian predator assemblages and species-habitat relationships within and among landscapes (e.g., References [46,47]). Avian predator abundance and the resulting predation pressure affect the composition and abundance of ground nesting bird species assemblages [15,110–112]. For example, Roodbergen, et al. [113] found that nest predation on eggs and chicks of five wading bird species has increased by >40% over the past 4 decades. However, adult survival rates have remained stable. Likewise, the decline in breeding success of ground nesting forest birds (capercaillie and black grouse) has been linked to nest predation by corvids [114,115]. Additionally, the role of mammal predation on ground nesting birds is of importance and should be carefully considered [116,117]. Thus, we also encourage macroecological studies on the assemblages and abundances of mammal predators.

From a spatial planning point-of-view, biodiversity conservation requires the maintenance of sufficient quality, size, amount and connectivity of patches of representative types of natural forests and cultural landscapes at multiple scales so that they form functional habitat networks, also termed ecological networks [118], or green infrastructure [7]. Unfortunately, changes in landcover patterns are already proving challenging for planners and managers to grasp [29], and trophic interactions are even more subtle and difficult to cope with. The need to consider a process, such as predation, including the distribution and abundance of predators and prey adds complexity to the planning and management towards securing functional habitat networks. Thus, the long-term restoration and maintenance of functional species habitat networks remains challenging.

The three Swedish landscapes studied (with higher abundances of corvids) are intensively managed for maximum sustained yield of food, feed and fiber, and have many land owners. The traditional hay-making methods that reduce the nutrient levels of the top soil have been replaced by high yield agricultural production utilizing artificial fertilizers. This has eliminated plant species that are unable to compete with the dense and extremely fast and rich growing grasses [119]. In addition, changes in the type, number of livestock/ha [120] and increased quality of fodder have changed the flora and fauna in Sweden. At the habitat patch level, the beneficiaries of agro-environmental schemes are individual farmers as business enterprises. This complicates co-ordination among neighboring land owners, which results in short-term commitments to manage individual landcover patches, which often have several land owners.

The differences in land use histories among countries provides opportunities to learn about the linkages between predator assemblages, land use intensification and the opportunities for conservation of ground-nesting focal species. Current and future transitions towards intensive land management in Europe's East (e.g., Nemunas Delta and Turov) imply threats to the functionality of habitat networks through the abandonment of traditional land use practices and the intensification of natural resource production (e.g., References [37,65]). This stresses the need to address the general trade-off between use and conservation of landscapes [121,122]. Encouraging collaborative learning among actors and stakeholders towards functional habitat networks using macroecological research in landscapes with different states and trends of landcovers and species populations is thus urgent [41].

## 5. Conclusions

This study reveals two clear macroecological patterns in the Baltic Sea Region's West and East: (1) The abundance of omnivorous corvid birds (e.g., magpie, jackdaw and hooded crow) was associated with the number of anthropogenic food resources among the case study landscapes; in contrast (2) the abundance of raptor species increased with decreasing land use intensities. Therefore, to secure functional habitat networks for biodiversity conservation we stress the need to also understand and manage trophic interactions and associated cascading effects on predators and their prey. Using multiple landscapes spanning across regions and countries with different development trajectories

provides a broader perspective on what needs to be considered when conserving or restoring functional habitat networks through planning and management in social-ecological systems.

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