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ORIGINAL PAPER

Bird conservation in the Carpathian Ecoregion in light of long-term land use trends and conservation responsibility

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Abstract Land use change alters species' abundance and distributions by affecting habitat availability and quality. The decline of bird populations worldwide is of major concern, and habitat protection and restoration are primary conservation actions. However, conservation decisions largely consider only short-term habitat changes and species' population dynamics in a given area. Disregarding long term modifications in species' available habitat, and the role of a given population for a species' global population may lead to misdirected conservation action. Our goal here was to combine the assessment of conservation responsibility, with that of century-long available habitat dynamics, in order to inform better conservation practice. We compiled available habitat data for 170 bird species in the Carpathian Region from 1860 to 2010 from historic maps and satellite data. We analyzed these species' range distributions, IUCN extinction risk and population trends, and we identified 29 species of high conservation responsibility, and all of them were forest or and grassland specialists. Furthermore, we found major land use trends including cropland abandonment and increase in forests and grasslands that resulted in increases in potential habitat for the species for which the Carpathians have high conservation responsibility. The loss of row-crop agriculture, on the other hand, reduced habitat for species for which the Carpathians do not have high responsibility, and thus subsidizing agriculture may not be warranted from a conservation perspective. More broadly, many regions worldwide are

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undergoing rapid land use changes, and we suggest that these should be analyzed relative to a given regions' conservation responsibility to see if there are opportunities for conservation, i.e., cases similar to the Carpathians, where conservation efforts 'only' have to foster current land use trends, and make them permanent, rather than to try to revert the loss of habitat.

Keywords Conservation responsibility \cdot Land abandonment \cdot Reforestation \cdot Historic available habitat

Introduction

Globally, landscapes are changing rapidly due to agricultural expansion and intensification, but also reforestation and land abandonment (Foley et al. 2005; Hansen et al. 2010; Munroe et al. 2013). Where these changes result in habitat loss (Newbold et al. 2015) and fragmentation (Jongman 2002; Jaeger et al. 2011) they are of concern for biodiversity conservation (Balmford et al. 2002; Green et al. 2005). However, conservation planning is rarely based on long-term habitat changes raising concerns about the shifting baseline syndrome (Schulte et al. 2005; Vera 2010), even though historical land uses can affect ecosystem structure and functioning, and ultimately biodiversity levels (Plue et al. 2009; Dullinger et al. 2013; Brudvig et al. 2013), and subsequent land use trajectories (Munteanu et al. 2015), for decades or even centuries. Furthermore, land use trends greatly affect the costs and level of effort necessary to provide more habitat. Areas where land use trends result in more potential habitat may represent conservation opportunities, whereas areas where land use causes habitat loss, will likely entail higher conservation costs, and may require different conservation actions. This is why long-term land use assessments are essential when selecting habitat management strategies (Swanson et al. 1994; Landres et al. 1999).

Typically conservation action is concerned with protecting those species and habitats that are at highest risk of extinction, and quite rightfully so, but is rarely considering for which species an area carries high conservation responsibility (Schmeller et al. 2008, 2012). The concept of conservation responsibility defines the responsibility of an area for the persistence or survival of species based on what part of a species distribution is located in that area, as well as species abundance or population trend (Keller and Bollman 2004; Schmeller et al. 2014). Not considering conservation responsibility in planning can result in conservation actions that are suboptimal if focused on species for which a given region could at best contribute *minimally* to global survival. Instead, taking conservation responsibility into account prioritizes those species or habitats for which conservation action in a given region would result in significant benefit for the persistence of the species at large (Keller and Bollman 2004). Thus to support biological diversity at broad scales, conservation action would benefit from considering both the conservation responsibility of the selected area (Keller and Bollman 2004; Schmeller et al. 2008) and long term habitat assessments (Swanson et al. 1994; Landres et al. 1999).

In Europe bird populations have been declining for several decades (Donald et al. 2001; Gregory et al. 2007). In landscapes dominated by agriculture, these declines are the result of intensification partly due to the Common Agricultural Policy (Donald et al. 2001, 2002). Grassland birds in particular have declined due to agricultural intensification, invasive species, and habitat alteration (Busche 1994; Skorka et al. 2010). Similarly, forest birds have declined due to loss of nesting habitat and forest disturbance



(Gregory et al. 2007; Wade et al. 2013; Sullivan et al. 2015). However, some landscapes are experiencing the opposite trend, and their land use is becoming less intensive (Baumann et al. 2011; Alcantara et al. 2013), offering opportunities for habitat recovery (Navarro and Pereira 2012; Ceauşu et al. 2015a). Indeed there have been population increases of some forest birds in parts of Eastern Europe (Reif et al. 2008). When land use becomes less intensive, the question for conservation is whether it is better to foster natural succession (Navarro and Pereira 2012) or to maintain low-intensity land use practices, which can have conservation benefits in their own right (Fischer et al. 2012). This trade-off among different conservation goals is particularly relevant in regions with widespread agricultural land abandonment.

In landscapes with decreasing land use intensity or where traditional farming has been maintained (Koleček et al. 2015), it may be beneficial for conservation to pay farmers to manage their land less intensively, and retain wildlife-friendly farming (Plieninger et al. 2006; Mikulcak et al. 2013; Hartel et al. 2013). However, retaining traditional farming practices may not be desirable in areas where the social structure of the farming communities has eroded (Figueiredo and Pereira 2011; Regos et al. 2016), and where there may be a real opportunity for rewilding (Navarro and Pereira 2012). Indeed, some regions of Europe, such as the Carpathian Mountains, have been suggested as potential candidates for rewilding, due to high rates of land abandonment, contiguous forest ecosystems, high mammalian and avian biodiversity, and presence of large carnivore and herbivore species (Navarro and Pereira 2012; Ceausu et al. 2015a, b). The question though is whether rewilding, which could greatly benefit forest species, should be the conservation goal throughout the Carpathian region, given that this would entail the likely loss of habitat for farmland species. Empirical evidence suggest that bird populations in Eastern Europe, and especially in the Carpathians, are declining at slower rates than in Western Europe (Verhulst et al. 2004; Gregory et al. 2007; Reif and Hanzelka 2016), most likely because land use intensity is lower there (Gregory et al. 2007; Reif and Hanzelka 2016). For this reason, the Carpathians may be a promising region on which to focus bird diversity conservation efforts in Europe. However, the historical landscape context and the conservation responsibility of the Carpathians remain largely unexplored, leading to potentially ill-informed conservation actions.

The question of what conservation actions are most effective in places with decreasing land use intensity is not just a theoretical one. The European Union supports substantial programs to address biodiversity conservation, including the preservation of low-intensity, high-natural-value farmland via agro-environmental payments (€4.44 billion/year between 2007 and 2012, European Court of Auditors 2011) and protection of species and habitats under the Natura 2000 conservation program (estimated €5.80 billion/year in 2012). Yet these efforts rarely consider long-term habitat dynamics for species of high conservation responsibility in the geographical regions where they are implemented (Keller and Bollman 2004; Schmeller et al. 2008, 2012). Information on the conservation responsibility of a region (Keller and Bollmann 2001; Keller and Bollman 2004) for a given set of species is essential for making conservation decisions, such as allocating agro-environmental payments towards regions that carry high conservation responsibility for farmland species, and allowing abandoned agriculture to reforest in regions with high responsibility for forest species.

Our overarching goal was to provide bird conservation recommendations for the Carpathian Mountains, based on historical and recent changes in habitat area for species of highest conservation responsibility.



- (1) How did habitat area for different bird species in the Carpathians change over the past 150 years?
- (2) For which bird species do the Carpathians carry the highest conservation responsibility at the European level?
- (3) What bird conservation strategies should be pursued, and what future land use trends would be most desirable for bird conservation in the Carpathians?

Methods

Study area

We studied the Carpathian Ecoregion (207,309 km²) which is the largest mountain range in Europe and a highly diverse landscape with rare old growth forests (Knorn et al. 2012), diverse cultural landscapes (Kozak et al. 2013b), and high biodiversity (Kuemmerle et al. 2010; Akeroyd and Page 2011; Pereira and Navarro 2015). The Carpathians are part of seven European countries, have a mean elevation of 850 m, with highest peaks reaching over 2500 m and mean annual temperatures between - 2 and 6 °C, depending on elevation (Kozak et al. 2013a; Munteanu et al. 2017b). The region experienced numerous shifts in land use over the last century, due to major changes in socio-economic and political conditions (Munteanu et al. 2015), including increasing forest cover and widespread agricultural abandonment (Munteanu et al. 2014). Contemporary land cover consists of forests (58%), grasslands (30%), agricultural fields (9%) and scattered settlements (Fig. 1a). Historically, forest cover was lowest during the 1930s (46%) and arable land was most widespread during the 1960s (27%, Munteanu et al. 2015; Munteanu et al. 2017a, b). Today, the main agricultural crops are wheat, corn, barley, potatoes, and sugar beets, mostly in small subsistence farms (Griffiths et al. 2013). Grasslands include pastures, hay meadows and wooded pastures, and they often have high biodiversity (Halada et al. 2008; Akeroyd and Page 2011; Hartel et al. 2013). Despite high forest disturbance and widespread spruce plantings during and after the Socialist regime (Griffiths et al. 2014; Munteanu et al. 2015), tree species diversity is high in the Carpathians. In river valleys, plains and on hillsides, deciduous woodlands (Quercus sp., Fagus sylvatica, Carpinus betulus, Populus sp., and Robinia pseudoacacia) are common. In the higher mountain landscapes, coniferous forests are dominant (Pinus sp., Picea abies, Abies alba, Munteanu et al. 2015). Lastly, the Carpathians have a growing network of protected areas, some of which are aimed at conserving habitat for bird species (Natura 2000), but effectiveness is highly variable (Butsic et al. 2017).

Data

We analyzed data for 252 bird species (BirdLife International and NatureServe 2014), and recorded attributes including range maps, IUCN Red List status, population trend at European level from 1990 to 2000, European level threats to the populations survival, and major habitat (i.e., the primary habitat used by the species for breeding and/or feeding) (Birdlife International 2016). Habitat data was available for 170 species of the 252 present in the Carpathians (Birdlife International 2016), so we restricted the analysis of habitat change to those species.



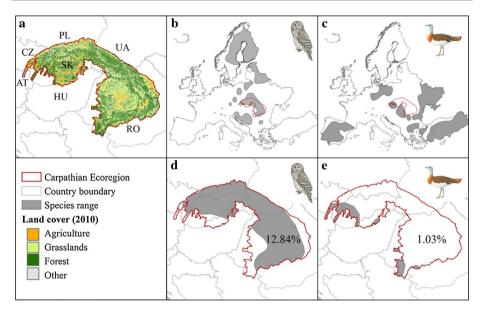


Fig. 1 a The Carpathian Ecoregion in Eastern Europe (CERI 2001) and land cover types in year 2010. Country codes *AT* Austria, *CZ* Czech Republic, *PL* Poland, *SK* Slovakia, *HU* Hungary, *UA* Ukraine, *RO* Romania. **b** European range map of Ural owl (*Strix uralensis*). 12.84% of the Ural owl's range falls within the Carpathians (**d**). **c** European range map of great bustard (*Otis tarda*). Only 1.03% of the bustard's range fall within the Carpathians (**e**)

We reconstructed the patterns of forest, grassland and agriculture throughout the Carpathian Ecoregion for 1860, 1930, 1960, 1985, 2000 and 2010. For this, we analyzed 51,648 points in a regular 2-km point sampling grid (Gallego and Delince´ 2010; Munteanu et al. 2015) and assigned one of the three land use types to each point in each year. We obtained land use data for the 1860s, 1930s and 1960s from historical topographic maps (Munteanu et al. 2015, 2017a) and land cover data for the years 1985, 2000 and 2010 from Landsat satellite data (Griffiths et al. 2013, 2014). Data quality and information content may vary across historical maps and due to low accuracy of historic maps. In parts of Romania and Hungary for 3,409 points, we could not distinguish agriculture from grassland in the 1860s, and therefore assigned these points the land use present in the 1930s (Kaim et al. 2016; Munteanu et al. 2017a). For comparability, we reclassified the major habitat data for each species (BirdLife International and NatureServe 2014; Birdlife International 2016) into three categories that matched our long term land cover data: agriculture, grasslands and forests (Supplementary Material S1).

Analysis

To determine the change in available habitat in the Carpathians for each of the 170 bird species since 1860s, we summed the area of the land use types that constituted that species' major habitat type for 1860, 1930, 1960, 1985, 2000 and 2010 (Fig. 1a, b). We restricted this analysis to the Carpathian portion of each contemporary range as defined by IUCN (BirdLife International and NatureServe 2014). Land use data for wetlands and open water



was not available for all time periods, which is why we excluded these habitat types from our analysis. We assumed that these habitats would not have influenced the overall trend greatly, because they only make up a small part of the landscape in the 1860s, when wetlands were well mapped (< 0.01% of the total mapped habitat). Nine wetland bird species were excluded from the analysis.

To determine the conservation responsibility of the Carpathians for each species, we considered three criteria: (a) if a species had a high proportion of its European range in the Carpathian Ecoregion (high proportional distribution) (CERI 2001), (b) if a species was listed by the IUCN as vulnerable (VU), near threatened (NT), endangered (EN), or critically endangered (CR), and c) if a species' population declined across Europe from 1990 to 2000 (BirdLife International and NatureServe 2014). We assumed that the proportional distribution of a species is a proxy for the relative importance of the region for the species' population viability, i.e., that regions conservation responsibility for that species (Keller and Bollman 2004; Schmeller et al. 2008). Because the Carpathians make up 3.1% of the total European landmass (excluding European Russia), we considered values < 3.1\% as a low proportion, and values > 3.1\% as a high proportion, of the species European range being located in the Carpathians (Fig. 1b-e). We gave special consideration to species with > 6.2% of their range in the Carpathians, following precedent (Keller and Bollmann 2001; Keller and Bollman 2004). We considered European population trends in determining conservation responsibility because if a species declined at the European level, but had a high proportion of its range located in the Carpathians, then the Carpathian Ecoregion could make a substantial contribution to the Europe-wide conservation of that species. We compared population trends during the period 1990–2000 with trends during the decade 2002-2012 (Birdlife International 2017) and for the species for which data was available found no substantial differences in the general trends (Supplementary Material S3). We checked if conservation responsibility values were comparable when considering the entire range of the species vs. only the species' major habitat types within its defined range by calculating the proportional distribution stratified by land use types, and found no substantial differences (Supplementary Material S2). By combining the proportion of the range with the IUCN extinction risk, and the population trend across Europe, we defined classes of conservation responsibility for the Carpathians (Supplementary Material S3). We defined species with a high percentage of distributional range (i.e. > 3.1%) in the Carpathians, IUCN status of concern, and declining population at the European level as species for which the Carpathians have high conservation responsibility. To understand which habitat types are important for the high conservation responsibility species, we analyzed the percentage of species' European range contained within the Carpathians, considering the major habitats used for feeding or breeding by each species. We compared the proportion of each species' range in Carpathians to the 3.1 and 6.2% thresholds.

To understand what conservation strategies could be pursued in order to ensure the conservation of high-responsibility species in the Carpathians, we reviewed the species threats at European level in relation to species' habitat changes. Descriptions of the major threat classes for each species were available from the IUCN Red List and Birdlife International (BirdLife International and NatureServe 2014). If a listed threat affected the species habitat at European level, but was, according to our results, not present in the Carpathians, we assumed that the conservation effort for protecting this species would be relatively low in the Carpathians compared to the rest of Europe, and therefore that the region could make a substantial contribution to the conservation of that species at large. However, if a threat was present in the Carpathians, then conservation may still be possible, but would likely entail a higher cost in order to address that threat. Finally, we identified land management



options that could minimize the number of threats for the high conservation responsibility species in the Carpathians.

Results

We found that available forest and grassland habitat increased substantially in the Carpathians since 1860 within the ranges of all bird species, and that agricultural habitat declined after 1960 (Fig. 3). We also found that of all species present, the Carpathians carry high conservation responsibility only for forest and grassland birds, and very low conservation responsibility for birds that rely on agriculture (Fig. 4). Furthermore, the main threats at the European level for the species of high conservation responsibility were agricultural intensification and natural system modification (Fig. 6). Forest and grasslands increased substantially in our study region since the 1960s and we suggest that there is high potential for successful conservation of forest and grassland species in the Carpathians, because more habitat has become available in the past 150 years for those species for which the Carpathians have the highest conservation responsibility. The Carpathians may thus represent a region of opportunity for conservation, where the focus should be to foster current land use trends and ensure that they do not revert.

We found that available forest and grassland habitat has increased across the Carpathian Ecoregion, and is now higher (48.1% forest and 31.8% grassland) than the 1860 baselines (47.7% forest and 20% grassland) (Fig. 2). This trend was consistent across all the countries in the study region (Supplementary Material S4). When analyzing the habitat use for all 170 species for which data was available, we found that the major habitat of 39% of all bird species is forest, for 27% it is grasslands, and only 2% rely on agriculture. The remaining species relied mostly on other habitats such as water, wetlands, or bare ground, or their habitat type was unknown (Fig. 4). When analyzing habitat trends within species ranges over time (1860–2010), we observed again a general increase in

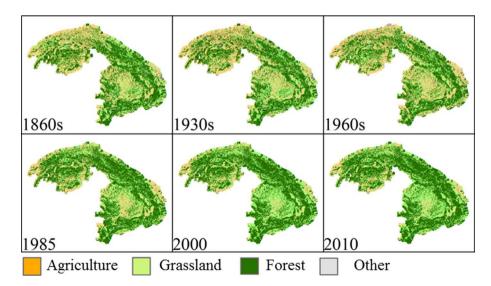


Fig. 2 Dynamics of available habitat across the Carpathian Ecoregion between 1860 and 2010



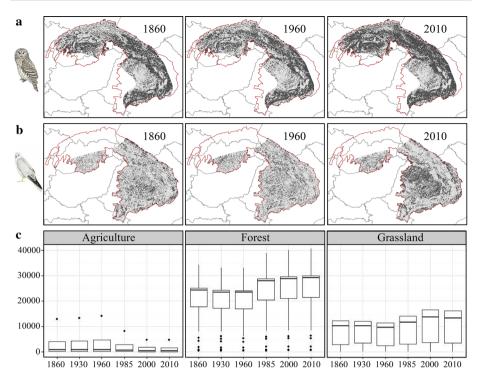


Fig. 3 a Available habitat (dark grey color) for the Ural owl (*Strix uralensis*) in 1860, 1960, and 2010. Species range is shown in light gray. **b** Available habitat (dark grey color) for the pallid harrier (*Circus macrourus*) in 1860, 1960, and 2010. Species range is shown in light gray. **c** Change in agriculture, grassland and forest available habitat (number of habitat points) for all species present in the Carpathians, by major habitat used. Double counting is possible if a species uses more than one habitat. Dynamics of other habitat types such as wetland or water are excluded

grassland and forest habitats, and a decrease in agricultural habitat (Fig. 3c). For example, the Ural owl (*Strix uralensis*) is a forest specialist, and the available habitat within its Carpathian range increased form 48% in 1860 to 58% in 2010 (Fig. 3a). Similarly, for the Pallid harrier (*Circus macrourus*), a grassland specialist, the available grassland habitat increased from 25% in 1860 to 33% in 2010 despite an initial decline (Fig. 3b).

When comparing the proportion of each species' range in the Carpathians with the proportion of the Carpathians in European territory (3.1%), we found that for 67% of the species, the proportion of their Carpathian range was higher than the 3.1% conservation responsibility threshold. Furthermore, for 7% of all species (19 species) the Carpathians made up more than 6.2% of their European range. Most of these species were forest or grassland specialists, and none relied on agricultural fields (Fig. 4).

Of all the 252 Carpathian bird species, the IUCN Red List deems 16 species as either vulnerable (VU), near threatened (NT), critically endangered (CR), or endangered (EN). When analyzing the European level population dynamics between 1990 and 2000 for the 252 species, we found that 33.7% (85 species) declined at European level. Of these, 55 had a high percentage of their range in the Carpathians, and 12 were of conservation concern (VU or NT) (Table 1).



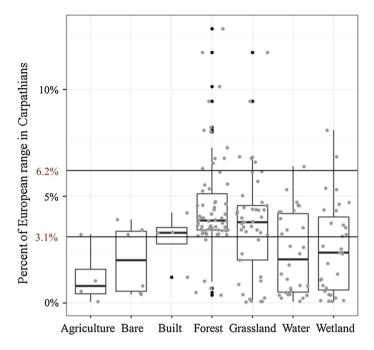


Fig. 4 Percentage of European range (y-axis) in the Carpathians for 170 species, by different habitat types (x-axis). Each grey dot represents a species associated with the respective habitat type. Black dots represent outliers. If a species used more than one habitat type, double counts are possible. Percentages are shown in relation to the 3.1% threshold (proportion of Carpathians from total European territory) and double that value (6.2%)

Overall, we identified 29 species of high conservation responsibility according to the proportion of their habitat in the Carpathians, their population trend, and their IUCN red list status (Table 1). Most of the 29 high conservation responsibility species require forest habitats (13 species), followed by grasslands (11 species), and other habitats (including wetlands, water and settlement areas, 9 species), and none require agriculture.

When analyzing the dynamics of available habitat for the species of high conservation responsibility, we found for all species an overall increase since 1860, particularly after 1960. Grassland species had small declines in available habitat since 2000, due to grassland conversions (Fig. 5). Of the species of high conservation responsibility in the Carpathians, the Eastern imperial eagle (*Aquila heliaca*), the lesser spotted eagle (*Clanga pomarina*), collared flycatcher (*Ficedula albicollis*), ring ouzel (*Turdus torquatus*), and red kite (*Milvus milvus*) require both forest and grasslands habitat for their survival, the rest are either forest (8 species) or grassland specialists (7 species).

When analyzing the major threats to species of high conservation responsibility at the European level, we found that the most frequent threats were related to agriculture and aquaculture, and natural system disturbance (Fig. 6, BirdLife International and NatureServe 2014). Farming, grazing and wood extraction were the most frequently cited threats. Of the 29 species, twelve were threatened by agricultural intensification and herbicide use, two by wood harvesting, and for thirteen species, no information on threats was available. Only lesser grey shrike (*Lanius minor*), snow bunting



Table 1 Species of high conservation responsibility in the Carpathians, and selected species characteristics

Scientific name	Common name	Order	Family	European population trend	% range in Carpathi- ans	IUCN Red List Status	IUCN Red Major habitat List Status	Habitat dynam- ics
Miliaria calandra	Corn Bunting	Passeriformes	Emberizidae	Decline	20.56	ГС	NA	u
Strix uralensis	Ural Owl	Strigiformes	Strigidae	Stable/fluctuating	12.84	ГС	Forest	×
Ficedula albicollis	Collared Flycatcher	Passeriformes	Muscicapidae	Increase	11.73	TC	Forest/grassland	Y
Tichodroma muraria	Wallcreeper	Passeriformes	Sittidae	Stable/fluctuating	11.62	ГС	NA	u
Nucifraga caryocatactes Spotted Nutcracker	Spotted Nutcracker	Passeriformes	Corvidae	Stable/fluctuating	10.13	ГС	Forest	y
Turdus torquatus	Ring Ouzel	Passeriformes	Turdidae	Stable/fluctuating	9.45	ГС	Forest/grassland	×
Dendrocopos syriacus	Syrian Woodpecker	Piciformes	Picidae	Decline	8.53	ГС	NA	u
Bonasa bonasia	Hazel Grouse	Galliformes	Phasianidae	Increase	8.22	ГС	Forest	×
Aquila heliaca	Eastern Imperial Eagle	Accipitiriformes	Accipitridae	Stable/fluctuating	8.09	VU	Forest/grassland	×
Picoides tridactylus	Three-toed Woodpecker	Piciformes	Picidae	NA	8.01	ГС	Forest	Y
Picus canus	Grey-faced Woodpecker	Piciformes	Picidae	Stable/fluctuating	7.27	ГС	Forest	y
Crex crex	Corncrake	Gruiformes	Rallidae	Stable/fluctuating	6.85	ГС	Grassland	y
Lanius minor	Lesser Grey Shrike	Passeriformes	Laniidae	decline	6.82	ГС	Grassland	Y
Clanga pomarina	Lesser Spotted Eagle	Accipitiriformes	Accipitridae	NA	6.78	ГС	Forest/grassland	y
Leiopicus medius	Middle Spotted Wood- pecker	Piciformes	Picidae	NA	6.77	ГС	Forest	>
Plectrophenax nivalis	Snow Bunting	Passeriformes	Emberizidae	Stable/fluctuating	09.9	ГС	Grassland	У
Bombycilla garrulus	Bohemian Waxwing	Passeriformes	Bombycillidae	Stable/fluctuating	6.54	ГС	Forest	y
Anser erythropus	Lesser White-fronted Goose	Anseriformes	Anatidae	Decline	6.39	VU	Other	u
Sylvia nisoria	Barred Warbler	Passeriformes	Sylviidae	NA	6.30	ГC	Forest	У
Circus macrourus	Pallid Harrier	Accipitiriformes	Accipitridae	Decline	6.16	NT	Grassland	y
Milvus milvus	Red Kite	Accipitiriformes	Accipitridae	Decline	6.13	NT	Forest/grassland	y
Coracias garrulus	European Roller	Coraciiformes	Coraciidae	Decline	5.70	L	Grassland	y
Acrocephalus paludicola Aquatic Warbler	Aquatic Warbler	Passeriformes	Sylviidae	Decline	5.37	ΛΩ	Other	n



Table 1 (continued)

Scientific name	Common name	Order	Family	European population trend % range in IUCN Red Major habitat Carpathi- List Status ans	% range in Carpathi- ans	IUCN Red List Status	Major habitat	Habitat dynam- ics
Aythya nyroca	Ferruginous Duck	Anseriformes	Anatidae	Decline	5.31	NT	Other	u
Falco vespertinus	Red-footed Falcon	Falconiformes	Falconidae	Decline	4.85	N	NA	п
Gallinago media	Great Snipe	Charadriiformes	Scolopacidae	Decline	4.36	NT	Grassland	y
Falco cherrug	Saker Falcon	Falconiformes	Falconidae	Decline	3.74	EN	Other	п
Limosa limosa	Black-tailed Godwit	Charadriiformes	Scolopacidae	Decline	3.42	NT	Grassland	y
Numenius arquata	Eurasian Curlew	Charadriiformes	Scolopacidae	Decline	3.20	NT	Other	п

Only species marked (y) in the habitat dynamics column were considered in our habitat dynamics analysis. For the rest of the species, habitat information was missing



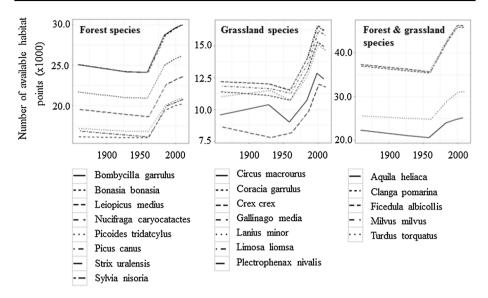


Fig. 5 Changes in available habitat for species of high conservation responsibility, by major habitat used

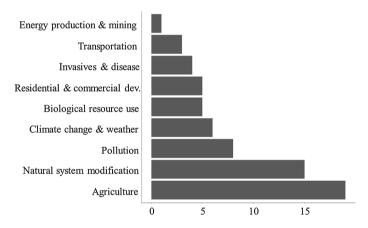


Fig. 6 Major threats to the species of high conservation responsibility as listed by IUCN (BirdLife International and NatureServe 2014). The x-axis represents how many species of high conservation responsibility in the Carpathians are affected by each threat class

(*Plectrophenax nivalis*) and ring ouzel were more affected by climate change than by habitat change.

Discussion

Regions where land use intensity is decreasing, such as the Carpathians, may offer opportunities for conservation because there is less competition for land, but the question is



whether conservation efforts should aim to restore natural habitats or to maintain low-intensity land use, and traditional agricultural practices. The answer to this question requires consideration of both long-term habitat dynamics and the conservation responsibility of a given region for the global population of a species (Keller and Bollmann 2001; Schmeller et al. 2012). Here, we assessed long-term habitat dynamics for bird species in the Carpathians, and identified the species for which the region has high conservation responsibility. We found that the species of high conservation responsibility require forest and grassland habitat to persist, but not agricultural land. For forest and grassland species, available habitat has increased since the 1860s, in contrast to trends in greater Europe, where their available habitat has decreased. Indeed, forest specialists have declined across Europe at a rate of – 18% between 1982 and 2003 (Gregory et al. 2007) while these species have increased in Carpathian countries, like the Czech Republic, in the same period (Reif et al. 2007). Our findings thus suggest that the Carpathians are a logical conservation stronghold for the 29 bird species of conservation concern that all depend on forest and grasslands as major habitat, for which the Carpathians have high conservation responsibility, and long-term land use trends are favorable.

Based on our results, we suggest that conservation action should be directed towards forest species and grassland species. Among the forest species, there are several woodpeckers, as well as Ural owl, and hazel grouse. We caution though that the conservation of forest birds depends greatly on the type of forests, and their structure. Many bird species require structurally heterogeneous forests for survival. For example, the Ural owl requires contiguous forest with a high proportion of deciduous and old trees (Kajtoch et al. 2015), the hazel grouse requires dense understory and alder (Aberg et al. 2003; Schaublin and Bollmann 2011), and most woodpeckers require old trees and snags (Lõhmus 2003; Roberge et al. 2008). Because woodpeckers are great indicators for forest bird diversity in Eastern Europe (Mikusiński et al. 2001), conserving these species will likely benefit many other Carpathian species. Unfortunately, despite being a stronghold for old-growth forests (Kozak et al. 2013b; Munteanu et al. 2015), extensive harvest and shifts to spruce and pine monocultures in the Carpathians (Knorn et al. 2012; Griffiths et al. 2014; Munteanu et al. 2015, 2016) likely have degraded habitat quality for high conservation responsibility species. Forest management should thus aim not just to restore forest cover, but also to increase native tree species diversity and forest stand complexity.

Four species in our analysis require woodland plus either grassland or wetlands. The increase in habitat availability that we found since 1860s for the Eastern imperial eagle, coincides with population rebounds in Slovakia, Hungary, and the Czech Republic (Demerdzhiev et al. 2011) after the late 19th and early 20th century (Salmen 1980). Across Europe, the Eastern imperial eagle is threatened by agricultural intensification (Hallmann 1996), but because land abandonment is widespread in the Carpathians and industrial agriculture is uncommon, we suggest that the region is well suited for the protection of this species, and species with similar habitat requirements such as red kite, lesser spotted eagle, and collared flycatcher. The Transylvanian plain, especially, represents a highly suitable landscape for these species due to its mosaic landscape of woodlands and open grasslands (Fischer et al. 2012; Hartel et al. 2013).

Last but not least, grassland birds should also be a focus of conservation actions in the Carpathians. While grassland species like the corn crake (*Crex crex*), lesser grey shrike (*Lanius excubitor*), and ring ouzel (*Turdus torquatus*), are declining across Europe, we found their available habitat in the Carpathians has increased since 1860, mostly due to agricultural abandonment. The available habitat trends revealed by our data match historical population dynamics (Salmen 1980; Elts 1997). One reason the Carpathians provide



more habitat for so many forest and grassland species is the agricultural abandonment since the collapse of the collective farming system (Kuemmerle et al. 2008; Griffiths et al. 2013; Hartvigsen 2014). At the European level, the majority of the threats to the Carpathians' species of high conservation responsibility are related to agricultural intensification, and herbicide use. Fortunately, of the Carpathian bird species, climate change negatively affects relatively few species while agricultural change and natural resource modification are far greater threats (Fig. 5). Although global climate change may have affected the ranges of some species analyzed, in the Carpathians these effects are relatively minor compared to the major land use changes since the 18th century, and the habitat gains may not be compromised too much by climate change in the foreseeable future (Kuemmerle et al. 2008; Griffiths et al. 2013; Munteanu et al. 2014).

Overall, we suggest that maintaining and enhancing both forests and grasslands would be best for bird conservation in the Carpathians, but maintaining row-crop agriculture would not. Forested areas located in the mountainous regions would benefit other species that prefer isolated habitat (Pereira and Navarro 2015), such as the lynx. Maintaining grasslands in Transylvania, and in the larger river valleys, where potentially wildlife-friendly livestock farming could persist, would contribute to the conservation of grassland species (Mikulcak et al. 2013; Hartel et al. 2013). Furthermore, protection of high mountain grasslands would preserve open-habitat species that rely on the diversity of these habitats (Halada et al. 2008; Bezák and Halada 2010) (Supplementary Material S5). In addition to birds, grassland conservation would benefit other taxa with high species richness in the Carpathians, such as plants and butterflies (Cremene et al. 2005; Schmitt and Rákosy 2007; Loos et al. 2014).

However, several challenges will have to be overcome in order to achieve these goals in the region (Supplementary Material S5). Maybe the most significant challenge is that the Carpathians Ecoregion spans several countries with different policies and attitudes towards conservation and land use management. Pan-Carpathian initiatives such as the Carpathian Ecoregion Initiative (CERI 2001) or the Carpathian Convention (www.carpathianconvention.org) can help bridge gaps between countries. Further, poverty in the region and the lack of conservation capacity could prove challenging for securing habitat strongholds for the species of high Carpathian conservation responsibility. Bottom up strategies for conservation, and eco-friendly tourism could help overcome these issues. Furthermore, there are some limitations to our approach, the most important one being the lack of historical species range maps. Because ranges might have contracted over time due to climate change or other environmental factors, our estimates of habitat change could be underestimated in cases of species whose ranges have expanded. However, we expect that the overall habitat change trends would remain unaffected.

Overall, three broad conservation messages for the Carpathian Ecoregion emerge from our analysis: (1) The region carries great conservation responsibility for forest and grassland species, and hence, conservation efforts should focus on these species and their habitats. (2) The conservation responsibility of the Carpathians for agricultural species is very low, and therefore cropland abandonment is a positive conservation trend in the Carpathians, as long as grasslands persist. (3) The observed increase in potential habitat provides a great opportunity for securing habitat strongholds for species that are declining elsewhere, as long as forest diversity, and structural elements such as dead wood and snags, are maintained.

More broadly speaking, our approach provides a simple tool that combines conservation responsibility (Keller and Bollmann 2001; Schmeller et al. 2012) with long-term habitat



dynamics in order to guide conservation actions, and identify regions of opportunity, i.e., those regions where land use trends favor species for which the region carries high conservation responsibility. Our results showed that land abandonment may be a positive trend for conservation in the Carpathians, and this may be true elsewhere, but probably not everywhere because abandonment has both beneficial and detrimental effects for biodiversity across the globe (Queiroz et al. 2014; Reif and Hanzelka 2016). However, we suggest that our approach to combine analysis of conservation responsibility and long-term land use trends is relevant everywhere to identify regions of conservation opportunities, and those regions where land use trends threatened species of high conservation responsibility, thereby providing additional information to target conservation efforts and tailor them to a given region.

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