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Conservation status of birds in habitats along a successional gradient from bare ground to forest

Václav Bystřický¹ · Lenka Dvořáková^{1,2} · Jiří Reif^{1,3}

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Abstract

Ecological succession creates a sequence of habitat types after an initial disturbance. In Central Europe, these types typically include a gradient of stages from bare ground to forest. Ecological communities differ between habitat types because some species are associated with a given type along the gradient. The conservation status of these communities provides information about environmental pressures acting upon the respective habitat types. Here, we focused on birds and compared three measures of their conservation status, namely population trend, Red List category, and legal protection, expressed at two different levels, national and European, among the habitat types. We used data from the mapping of breeding bird occurrences in 42 abandoned military training sites in Czechia covering the entire successional gradient. In these areas, we identified 423 habitat polygons, each representing one of the following habitat types: bare ground, grassland, sparse scrubland, dense scrubland and forest. In general, birds recorded in forest had the most favorable conservation status, while birds recorded on bare ground and grassland had the least favorable; birds of both types of scrublands showed intermediate values. This corresponds to recent findings of the suitability of forest management for bird populations in Central Europe on the one hand and the adverse impacts of various changes in the human use of open habitats on the other. We observed a general agreement in the different measures, indicating that population trends are likely used for Red List categorization, which further serves to select species for legal protection. However, exceptions to this general pattern suggest that the listing and establishment of legal protection do not adequately reflect population changes and need more frequent updating.

Keywords Population trend · Red List · Legal protection · Habitat · Ecological succession · Bird community

Introduction

Ecological succession is a key process in ecosystem dynamics (Prach & Walker, 2011). In the Northern temperate zone, ecological succession is generally represented by gradual changes from open treeless habitats created by natural or human disturbances to mature forest stands covered by tall trees (Coradini et al., 2022). In the landscape context of Central Europe, the succession of habitat types along this gradient is mostly driven by human land use (Prach et al.,

☑ Jiří Reif jirireif@natur.cuni.cz 2013; Pruchniewicz, 2017), whereas the influence of natural disturbances is confined to remnants of wilderness areas such as protected old-growth forests (Frankovič et al., 2021). Therefore, linking species occurrences to respective habitats along the successional gradient can be informative for identifying land uses that potentially affect populations of those species.

The Central European successional gradient can be discriminated into five main habitat types: bare ground, grassland or cropland, sparse scrubland, dense scrubland, and forest. Bare ground is an initial successional stage occurring immediately after a disturbance event (Prach et al., 2001). They were formerly often created by overgrazing on extreme sites—xeric thermophilous and nutritionally poor grasslands (Varga et al., 2021). After the widespread cessation of pasturing on such extreme sites in the second half of twentieth century due to its unprofitability, bare ground currently occurs only rarely, as a by-product of other human activities such as military training or off-road rides (Heneberg et al.,

¹ Institute for Environmental Studies, Faculty of Science, Charles University, Prague, Benátská 2, 128 01 Praha 2, Czechia

² Beleco, z.s., Prague, Czechia

³ Department of Zoology, Faculty of Science, Palacky University Olomouc, Olomouc, Czechia

2016). Grassland and cropland are the most widespread open habitat types in Central Europe due to their maintenance by modern agriculture: cattle pasturing, mowing of meadows and the cultivation of arable land (Kolář, 2001). Sparse scrubland typically occurs on abandoned open habitats several years after the cessation of agricultural management (Prach & Pyšek, 2001). Over time, shrubs mature and grow, so sparse scrubland transforms into dense scrubland. The progress of this transformation depends on local climatic and soil conditions as well as propagule pressure, taking longer at more extreme and remote sites (Prach & Řehounková, 2006). Dense scrubland is the successional stage before the transition to forest, which is considered the final stage of ecological succession in Central Europe (Prach et al., 2016). Both types of scrublands occur frequently in the Central European landscape due to the widespread abandonment of farmland in less profitable areas (Kupková et al., 2021). Forest land is strictly protected from transformation to other habitat types, so its area has been gradually increasing in Central Europe (McGrath et al., 2015), with a major proportion managed toward increasing maturation (Riedl et al., 2020).

The habitat types along this successional gradient may differ in the species composition of their ecological communities because some species show associations with respective habitat types along this gradient (Reif et al., 2013). These differences in habitat associations between species probably result from their evolution in different environments and maintenance of their habitat preferences due to the conservatism of ecological niches (Pearman et al., 2014). At the same time, species in these communities can differ in their conservation status, reflecting the pressures acting upon respective habitat types. In this respect, it is interesting to ask which habitat types host the species of the lowest and the highest conservation status, respectively.

Here, we performed a comparison of conservation status among the respective habitat types along a successional gradient in Czechia, a Central European country, using birds as study organisms. Birds show conspicuous variability in their habitat associations (Storchová & Hořák, 2018) and a high level of species turnover along successional gradients (Craig et al., 2015). In addition, their conservation status can be expressed by several different measures. First, long-term population trends quantify the rates of population increase or decrease over a given period (Wauchope et al., 2021). If they remain unchanged, decreasing trends lead to population extinction, so the trend value serves as an early warning signal of potential extinction risk (Reif, 2013). Second, the Red List category is based on several criteria including population trajectory, population size and the area of occupancy, providing a more complex evaluation of extinction risk accompanied with an estimate of the remaining time to extinction (Mace et al.,

2008). Third is the level of a species legal protection, which often depends on its Red List category or population trend, but also considers social aspects or economic interests (Evans et al., 2013). Therefore, some protected species may be unthreatened, while some threatened or declining species may remain unprotected (Voříšek et al., 2008). We considered respective measures of conservation status at both national and European levels to uncover the habitat types that are important for bird conservation from both regional and continental perspectives.

We performed our comparison by investigating bird assemblages in the successional habitat types present in abandoned military training sites. Most of these sites contain the whole gradient spectrum, making such a comparison feasible. The aims of this study were (i) to express bird conservation status in different habitat types along the successional gradient from bare ground to forest and to compare the status among the habitat types; (ii) to compare patterns along the gradient between different measures of conservation status, i.e., population trend, Red List category and legal protection; and (iii) to compare the patterns between the measures expressed using national (Czech) and continental (European) evaluations of conservation status.

Methods

Study area and study sites

We focused on 42 abandoned military training sites in Czechia. The sites were of smaller size (mean area = 91 ha \pm standard deviation = 74 ha) and scattered all over the country from low to mid latitudes (Fig. 1), forming a representative sample of all such areas available. The sites were used for military training until the 1990s (Reif et al., 2011), which created a heterogeneous habitat mosaic under various disturbance levels from bare ground to forest (Cížek et al., 2013). After abandonment by the army, most of the sites were left unmanaged, leading to ecological succession toward a closed forest (Čížek et al., 2013). However, some sites (or parts of some sites) were used for human leisure activities whose impacts were similar to military training (off-road rides, motocross, rides of historical armed vehicles), and some others were managed by nature conservation authorities or non-governmental organizations, with shrub removal, mowing, cattle pasture or rewilding (Marhoul et al., in prep.). Both of the leisure activities and conservation management effectively slowed down the successional changes (Konvička et al., 2021). As a result, the sites hold variable proportions of habitat types along the entire successional gradient from bare ground to forest.

Fig. 1 Abandoned military training sites in Czechia included in this study. Numbers correspond to the site IDs in Table S1



Bird occurrence mapping

We performed intensive mapping of bird occurrences on all 42 abandoned military training sites during the breeding season in 2020 or 2021. Every site was visited twice per season (once in late April/early May and once in late May/ early June) to record both early and late breeders (Bibby et al., 2000). During each visit, an observer slowly walked through the site several times to cover its whole area and recorded the position of every bird individual on an aerial photograph using the ObsMapp application (https://obser vation.org/apps/obsmapp/). Such spot mapping enabled the accurate detection of bird occurrences, avoiding multiple counts of the same individuals; flyovers (i.e., birds passing over the site without landing) were not recorded. The visits were performed early in the morning (from sunrise to 10 a.m.) under favorable weather conditions (no heavy rain or strong wind). As a result of this mapping, we obtained maps of each abandoned military training site with the positions of all recorded birds.

Habitat mapping

For every abandoned military training site, we created a map of habitat types at a scale of 1:1000. The maps were made by the manual processing of aerial photographs (ČÚZK, 2020) corresponding to the years when bird occurrence mapping was performed at a given site, i.e., 2020 or 2021. The processing was performed in the QGIS 3.16.11 software (QGIS Development Team, 2022), with the polygons of individual habitat types recognized and subsequently verified in the field. We discriminated five habitat types following Reif et al. (2013): bare ground (N=15 polygons), grassland (N=49), sparse scrubland (stands of discontinuous woody plant vegetation up to 3 m in height; free walking through was possible; N=130), dense scrubland (continuous stands of woody plant vegetation up to 3 m in height; walking though was not possible without moving or cutting branches; N=122), forest (continuous strands of woody plant vegetation up to 3 m height; N=107). The polygons were exclusive, so their areas never overlapped, and they covered the entire area of each abandoned military training site. In total, we discriminated N=423 polygons (Table S1), with a mean per site of 10 (range from 5 to 18).

Measures of bird conservation status

For each of the recorded bird species (N=81), we determined six measures of its conservation status—three for national level of Czechia and three for the continental level of Europe (Table S2). *Population trend* was obtained at the national level from Storch et al. (2023), who estimated the trend of each species as the slope of a regression line through its annual population indices from 1982 to 2019 based on country-wide breeding bird monitoring data. This quantifies the mean annual population change over the focal period. At the continental level, we extracted the values from Keller et al. (2020), who calculated the change in European breeding distributions between two continent-wide mapping periods corresponding (in most countries) to the 1980s-early 1990s (the first period) and to 2014–2018 (the second period). This population change was expressed at a scale from -1 (the largest possible decrease) to + 1 (the largest possible increase).

Red List category was obtained from the national Red List of Birds in Czechia (Chobot & Němec, 2017) and from the European Red List of Birds (BirdLife International, 2021), respectively. Following Koleček et al. (2014a), we transformed respective categories to numeric values as follows: least concern—0, near threatened—1, vulnerable—2, endangered—3, critically endangered—4.

Legal protection at the national level resulted from the latest version of the protected species list (https://www.mzp. cz/www/platnalegislativa.nsf) according to the Czech Nature Protection Law (Anonymous, 2021). At the European level, we used Annex I of the Birds Directive of the European Union, recognizing the species of European conservation concern (Koschová et al., 2018). In the case of Czechia, the nature protection law discriminated among different levels of protection, so we could assign 0 to unprotected species, 1 to protected species and 2 to strictly protected species. In the case of Annex I, we could only assign the value of 0 to unlisted species and the value of 1 to listed species.

Birds in habitat polygons

In the QGIS software, we overlapped bird records with the habitat map for every abandoned military training site, obtaining a list of bird individuals recorded in respective habitat polygons at each site (Fig. 2). Following Reif et al. (2022a), we considered a bird list for one habitat polygon as a bird assemblage. For each bird assemblage, we calculated the mean value of each measure of conservation status. For this calculation, we used the proportions of individuals of respective species relative to all bird individuals recorded in a given polygon as weights, so that more abundant species had a higher weight (Reif et al., 2022a). The obtained assemblage-level means of respective measures of bird conservation status in individual habitat polygons (Table S1) were used as response variables in further analyses.

Statistical analysis

We used linear mixed models (LMMs) to relate respective measures of conservation status to habitat type. In each LMM, a given measure of conservation status was the response variable, habitat type was the fixed-effect categorical explanatory variable with five levels corresponding to respective habitat types, and the name of the abandoned military training site was the random intercept. The replicates were individual habitat polygons, so this random effect accounted for the potential non-independence of polygons at the same site. Since each measure of conservation status was included in a single model, we ran six LMMs in



Fig. 2 An example of an abandoned military training site (Přáslavice, site 37 in Fig. 1) with polygons of different habitat types overlapped by bird records. Note that bare ground was not present at this site. The increasing color intensity reflects the increasing successional stage of respective habitat types

total. For each model, we tested for the presence of spatial autocorrelation in the residuals to uncover potential nonindependence violating assumptions of statistical testing. However, no signs of such a violation were detected (Fig. S1). We also plotted the residuals vs. fitted values for the respective models to judge their normality (Fig. S2). Statistical analyses were performed in R version 3.6.2 (R Core Team, 2019) using the packages 'nlme' (Pinheiro, 2021), 'MuMIn' (Bartoń, 2020) and 'ncf' (Bjornstad & Cai, 2020).

Results

The habitat types differed in the mean population trends of birds recorded in individual habitat polygons (Table 1). The patterns were very similar at the national and European levels. In both cases, no habitat type expressed significantly negative mean population trends for the recorded birds (Fig. 3a, b). However, birds recorded in bare ground and grassland habitats had mean trends that were not statistically different from zero, while the mean trends of birds recoded in sparse scrubland, dense scrubland and forest were significantly positive (Fig. 3a, b). Bird population trends were most positive in forest at both national and European levels (Fig. 3a, b), but the difference from dense scrubland was insignificant at the European level (Fig. 3b). Sparse and dense scrubland did not differ from each other statistically, and the mean population trends of birds recorded in these habitat types were intermediate between open habitats and forest (Fig. 3a, b). At the same time, dense scrubland tended to have generally more positive mean population trends of birds, especially at the European level, while the mean trend in sparse scrubland did not differ from the mean trend in open habitats (Fig. 3a, b).

Mean values of the Red List categorization of the recorded birds differed among habitat types (Table 1) and showed partly similar patterns to those found for population trends, with bare ground and grassland hosting generally more threatened bird species than both kinds of scrubland and forest (Fig. 3c, d). However, important differences were

 Table 1 Characteristics of linear mixed models relating respective mean values of different measures of the conservation status of birds recorded in individual habitat polygons to the habitat type of these polygons. A single model was run for each measure

Measure of conservation status	df	F	Р	Pseudo- <i>R</i> ²
National population trend	4, 377	9.6	< 0.001	0.13
European population trend	4, 377	9.84	< 0.001	0.15
National red list	4, 377	5.54	< 0.001	0.09
European red list	4,377	3.64	0.006	0.04
National legal protection	4,377	4.12	0.003	0.06
European legal protection	4, 377	4.96	< 0.001	0.07

observed between the national and European levels. According to the national Red List, the most threatened species were recorded in grassland, and their threat was higher than that of species in both kinds of scrubland and in forest (Fig. 3c). The mean threat of species in bare ground was not significantly different from zero or from the other habitat types (Fig. 3c). In contrast, at the European level, the mean threat of recorded birds was highest in bare ground and all other habitat types showed a significantly lower threat (Fig. 3d). The least mean threat of recorded birds was observed in forest, which was not even different from zero at the national level (Fig. 3c). However, the differences from other habitat types except bare ground were not significant at the European level (Fig. 3d).

Across the focal habitat types, the mean legal protection of recorded birds differed (Table 1) and the patterns along the successional gradient were congruent between the national and European levels. Specifically, the most strictly protected species were recorded in grassland, whereas forest hosted mostly unprotected species (Fig. 3e, f). Moreover, both kinds of scrubland had intermediate levels of mean legal protection of birds (Fig. 3e, f). The mean legal protection of birds recorded in bare ground could also be considered as intermediate, but it did not differ significantly from all remaining habitat types (Fig. 3e, f).

Discussion

The conservation measures studied here showed considerable differences between habitat types along the successional gradient. These differences resulted from differences in the bird community composition between the habitat types, which are largely driven by birds specialized to specific habitats (Reif et al., 2010). However, many species are habitat generalists that occur in multiple habitat types (O'Reilly et al., 2022), and such species can obscure such patterns in our data. In addition, birds are relatively large and mobile organisms (Fandos et al., 2022) that can move easily among habitat polygons in the study areas. From this perspective, it should be kept in mind that in the patterns, we discuss below, the focal habitat types host overlapping bird communities represented by species with more or less strong habitat associations, and only a handful of species are confined to a single type.

Changes of bird conservation status along the successional gradient

Our results showed that across all measures of bird conservation status, the status was generally higher in early successional habitat types (grassland, bare ground) compared to the late successional types (scrubland, forest). Fig. 3 Bird conservation status in respective habitat types along the successional gradient from bare ground to forest. Conservation status is described by three different measures: population trend (a, b), Red List category (c, d) and legal protection (e, f), each expressed at the national level (a, c, e) and European level (**b**, **d**, **f**). Mean values and standard errors estimated by linear mixed models are shown. Differences from zero are depicted by an asterisk, differences between individual habitat types by different lower-case letters. The increasing color intensity reflects the increasing successional stage of respective habitat types



Fig. 3 (continued)



This pattern may be explained by differences in human pressures on these habitat types and by their different availability in the Central European landscape.

Bare ground is rare both in Europe and Czechia (Tropek et al., 2013), which inevitably results in a rarity of the species associated with this habitat type. As rarity is one of the metrics used for Red List categorization (Mace et al., 2008) and legal protection (Anonymous, 2021), this results in higher Red List and legal protection categories for the species recorded in this habitat type. The low proportion of bare ground was also an important aspect of habitat composition in the abandoned military training sites in our sample, as it accounted for only 15 out of 423 habitat polygons. As a consequence, measures of the conservation status of bird assemblages in this habitat type had large standard errors which often widely overlapped with the other types. On the other hand, rarity cannot explain the low values of mean population trends for birds recorded on bare ground, because these trends are unrelated to species' population size or area of occurrence (Reif, 2013). Therefore, some pressures leading to the decreasing quality of this habitat should exist. One possibility is the degradation of bare ground habitats due to high nitrogen deposition (Hůnová, 2016), which facilitates plant growth leading to rapid encroachment (Ochoa-Hueso, 2017) and may inhibit the population growth of bird species associated with this habitat type.

The high conservation status of birds recorded in grassland can be explained by land use intensification. In Czechia, grasslands expanded due to the abandonment of arable land in the early 1990s, which was also associated with improvements in the populations of some grassland birds (Reif & Hanzelka, 2016). However, since that time, many grasslands have become intensively managed for production purposes, and this was further magnified after EU accession in the mid-2000s (Reif & Vermouzek, 2019). This is likely the case in other Central and Eastern European countries as well (e.g., Sanderson et al., 2013), which may be reflected in the mean trend of zero at both national and European levels for birds recorded in grassland in our data. This unfavorable population status probably resulted in a response of nature conservation authorities because both national and European protection levels are higher in species recorded in grassland than in those recorded in other habitat types.

In contrast to bare ground and grassland, birds recorded in forest had the most positive population trends, were least threatened according to the Red List, and had the lowest levels or even absence of legal protection. This pattern implies that forest birds generally benefit from current forms of human land use. Forest management is probably one of the most important aspects of this, as several recent studies have reported its positive influence on populations of Central European forest birds (Reif et al., 2022b; Schulze et al., 2019). Such management is characterized by a limited size of clear cuts, long rotation periods and the obligatory presence of broad-leaved tree species in coniferous stands (Riedl et al., 2020). The suitability of this management is further supported by observations of the detrimental impacts of forestry in other Northern temperate regions with different management approaches, such as the creation of extensive clearcuts (Betts et al., 2022). On the other hand, we note that forest polygons in our dataset were mainly represented by small patches surrounded by open habitats or situated at the edge of larger forest blocks extending beyond the study sites. Such conditions are not suitable for the occurrence of threatened forest specialists such as the Black Stork (Ciconia nigra) or Red-breasted Flycatcher (Ficedula parva) (Chobot & Němec, 2017). If our sample contained interior habitats of large forests, it is possible that the conservation status of the recorded birds would be less favorable. However, Czech forest birds have shown positive population trends even when all breeding species including rare specialists are considered (Koleček et al., 2010), so we do not believe that the pattern in our data would change significantly if forest interiors were sampled.

Both types of scrublands typically had a conservation status of recorded birds intermediate between forest and open habitat types. This could have been caused by an overlap of species pools, since scrubland can host both forest birds (e.g., European Robin Erithacus rubecula) and grassland birds (e.g., Whinchat Saxicola rubetra) (Keller et al., 2020). As the conservation status of these bird groups differs markedly (see above), their mixing may have resulted in the intermediate mean values. However, as some species (such as the Barred Warbler Sylvia nisoria or Red-backed Shrike Lanius collurio) are specifically confined to scrubland habitat (Storchová & Hořák, 2018) and avoid the other habitat types, there might be also other factors involved in explaining the observed patterns in conservation status. For example, as scrubland is a transitional habitat emerging on abandoned and unmanaged open habitats, it is possible that scrubland birds benefit from farmland abandonment and subsequent shrub encroachment, which occurred at the end of twentieth century in Czechia due to deep socioeconomic changes in the early 1990s (Kupková et al., 2021). Due to the relatively long time that has elapsed since the occurrence of this abandonment, resulting in vegetation maturation at such abandoned sites (Kopecký & Vojta, 2009), one might expect more positive trends and lower threat and protection levels for birds recorded in dense scrubland than in sparse scrubland. This is exactly what we observed in our data, even though the differences were not significant for most measures.

Differences between measures of bird conservation status

Despite the fact that our three measures of conservation status somewhat differed in their fundamentals, they showed largely congruent patterns across the habitat types. This might indicate the possibility to use of one measure to infer aspects of the others. Specifically, population trends should serve for the classification of species into Red List categories (Mace et al., 2008), which can then be used for the establishment of legal protection (e.g., Bullock et al., 2022). From this perspective, it is interesting to focus on deviations from this congruence. At the national level, we saw large similarities between the Red List and legal protection, indicating that the protected species lists are updated according to prior threat classifications. This is a positive message indicating that protection is based on scientific grounds. However, patterns for both Red List and legal protections differ from the pattern for population trends across habitat types, where grassland birds showed the highest mean threat and protection levels, but not the most negative trends. This might have been caused by establishment of new agri-environmental schemes for grasslands that may have partly ameliorated the intensive agricultural use of this habitat (Kuna, 2021). Such a recent improvement may not yet be reflected by the Red List and legal protection statuses. Effective legal protection might have led to the same effect, resulting in trend improvement just due to this protection (Koleček et al., 2014b).

At the European level, the patterns were congruent between population trend and legal protection, but the Red List categorization largely deviated. Specifically, the threat level of species recorded on bare ground patches was much higher than that of species in the remaining habitat types. This pattern may reflect a particular risk for this habitat type in Europe. However, we should keep in mind that our dataset sampled only a handful of species that appear on the European Red List of Birds, namely the Lapwing, Quail, and Turtle Dove. Although all these species use bare ground for breeding or feeding, the pattern in our data could also have resulted from their coincidental occurrence in this habitat type and the generally low numbers of birds recorded on bare ground, making these species particularly influential. Therefore, we should take the high threat level for bare ground according to the European Red List with caution.

Differences between national and European levels

Respective measures of bird conservation status were expressed at the national and European levels to learn whether factors underlying the changes of these measures along the successional gradient were the same at regional and continental scales. A clear congruence in patterns across the habitat types was observed in legal protection at national and European levels. This correspondence suggests that listing species as protected is based on similar principles at both spatial levels. In some European countries, national protected species lists are simply inferred from the European listing (Koleček et al., 2014b), but this is not the case of Czechia where legally protected species are defined according to national requirements (Anonymous, 2021). Therefore, it is more likely that the legal protection in Czechia is a reaction to the same threating factors as those that are reflected by the European legal protection, namely hunting, land use change and climate change, that are recognized as the key threats to birds globally (Ducatez & Shine, 2017). This possibility is also supported by the patterns observed in the population trends, with the clear correspondence between the national and European levels indicating the impacts of similar drivers.

In contrast, marked differences were found in the case of Red Lists, with the most threatened birds at the European level were identified on bare ground, but at the national level in grassland. This difference suggests differences in the significance of the underlying drivers. Specifically, it seems that in Czechia, the intensification of grassland use is a more serious threat to birds than the degradation and loss of bare ground, while this is not the case in Europe. This contrast may be due to regionally variable land use intensity in Europe, where large areas of extensively used grasslands exist and hold viable population of grassland birds (Marcolin et al., 2021; Sutcliffe et al., 2015). Therefore, the grassland birds recorded in our study area and considered as threatened in Czechia may be not Red Listed in Europe. The high mean value of threat at the European level for species recorded on bare ground may have been affected by the low number of species in our dataset that appear on the European Red List of Birds at the same time (N=3). As bare ground polygons were generally species-poor (hosting 3.4 species on average compared to more than 10 species in other habitat types), coincidental occurrences of one or more of these three species in these polygons could have greatly ameliorated the mean threat of the assemblage.

Conclusion

Our analysis of data on bird occurrence collected in habitat types along a successional gradient from bare ground to forest at 42 abandoned military training sites in Czechia indicted more favorable conservation status of birds recorded in late successional habitats, namely forest, than in early successional habitats, namely grassland. These differences can be explained by different impacts of the use of these habitats by humans: whereas grassland birds suffer from agricultural intensification, forest birds benefit from forest management. Different measures of conservation status showed largely corresponding patterns, indicating that scientific data (population trend analysis, threat level classification) is indeed used for listing the species as protected. Despite this, some deviations in the patterns for Red List status and legal protection from those for population trends suggest that both of the former measures should be more frequently updated using the most recent population trend information available. Similar patterns were also observed for national and European level measures of conservation status, implying that bird populations are influenced by similar drivers at the regional and continental scales.

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