Tuexenia 41: 273–297. Göttingen 2021.
doi: 10.14471/2021.41.006, available online at www.tuexenia.de

Semi-open landscapes of former military training areas are key habitats for threatened birds

Halboffene Landschaften ehemaliger militärischer Übungsplätze sind wichtige Lebensräume für gefährdete Vogelarten

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Abstract

Military training areas (MTAs) show high numbers of rare and threatened species and diverse habitat patterns due to low nitrogen input and heterogeneous disturbance dynamics caused by military training activities that produce fine-scale landscape mosaics. Since the 1990s, major parts of MTAs in Europe have been decommissioned. In Germany, most of them were transferred to the national natural heritage now facing the challenge of developing comprehensive conservation management strategies. In order to elucidate their current conservation value in terms of habitat patterns and associated breeding birds we selected 14 former MTAs (c. 200 km²). We defined semi-open landscapes as sparsely wooded (> 20−46% wood cover) to densely wooded (> 46−68%) transition zones between open land and forests. Out of 6,476 breeding bird territories in total, the guild of birds associated with semi-open landscapes was exceptionally large, accounting for 61% of the total and 71% of all threatened birds, while the total semi-open area made up only 28% of the study areas. Six selected keystone species (*Anthus trivialis*, *Caprimulgus europaeus*, *Emberiza citronella*, *Lanius collurio*, *Lullula arborea*, and *Sylvia nisoria*) depended on different species-specific key resources (optimal wood cover, single or combination of habitat types). We concluded that preserving/restoring such semi-open landscapes requires large-scale management approaches towards mosaics of different successional stages or structural elements with varying wood cover and associated habitat types, and should be adapted to the desired keystone species. Promoting combined open land/woodland management of semi-open landscapes should become a policy priority for adapting EU Common Agricultural Policy (CAP) to the needs of bird conservation.

Keywords: European Birds Directive, habitat mapping, Red List of threatened species, succession

Erweiterte deutsche Zusammenfassung am Ende des Artikels

Manuscript received 31 January 2021, accepted 06 June 2021
Published online 31 October 2021
Co-ordinating Editor: Martin Diekmann

1. Introduction

Military training areas (MTAs) may harbour an unusually high biodiversity (AYCRIGG et al. 2015) and large numbers of threatened species (WARREN et al. 2007, REIF et al. 2011, ČÍŽEK et al. 2013). The European Commission's Natura 2000 program recognised the importance of MTAs for the conservation of threatened habitats and rare and endangered species (GAZENBEEK 2005). Their high biodiversity values are related to heterogeneous disturbance regimes generated by military training that produces mixtures of regularly and heavily disturbed, irregularly disturbed and largely untouched portions of MTAs, resulting in unique and highly dynamic fine-scale landscape patterns (WARREN et al. 2007). These largely resemble traditional land-use forms in historical central European landscapes, which had originally been maintained by extensive management with low nitrogen input and high temporal and spatial variation of disturbance, creating a fine-grained mosaic of habitats (WARREN et al. 2007, BUŠEK & REIF 2017). That contrasts with the majority of modern cultural landscapes in Europe where, due to specialisation in agricultural production and simplification of cropping systems (STOATE et al. 2009), disturbances usually occur in relatively large areas in a homogeneous fashion of constant frequency, intensity, and periodicity of human impact.

Since 1989, about 1.5 million ha of MTAs have been decommissioned due to international disarmament agreements in a unified Europe on both sides of the former Iron Curtain (ELLWANGER & REITER 2019). In Central Europe, open habitats like grasslands, heathlands, and inland dunes of the atlantic and continental biogeographical regions, reported as habitat types of Annex I of the European Habitats Directive (92/43/EEC), are located almost exclusively in both actively used and decommissioned MTAs (GAZENBEEK 2005, ELLWANGER & REITER 2019). However, particularly pioneer plant communities, such as dry acidic grasslands, dramatically decreased for the benefit of later successional stages after the abandonment of MTAs (JENTSCH et al. 2009). To halt this decline, in Germany, 120,000 ha of decommissioned MTAs of high conservation value became part of the national natural heritage scheme (BMU 2017). Since 2009, this land was transferred to become private property of environmental foundations and conservation organisations. Although major efforts were made for conserving biodiversity (e.g., SCHULZE et al. 2015, LORENZ et al. 2016), the new land owners still face the challenges of keeping land open under the situation of often heavy ammunition loads and of substituting the disturbance regimes on former MTAs by re-establishing dynamic small-scale, semi-open landscape patterns by civil measures (ELLWANGER & REITER 2019). Implementing such an alternative management requires comprehensive knowledge of the dependency of target species on the specific forms of suitable landscapes that need to be maintained or restored.

In this study, we used the guild of birds associated with semi-open habitats as target species assemblage for the management of decommissioned MTAs transferred to the national natural heritage. Typical representatives of the semi-open bird guild are European Nightjar (*Caprimulgus europaeus*), Red-backed Shrike (*Lanius collurio*), and Woodlark (*Lullula arborea*). Birds are highly valuable indicators of biodiversity, because they represent various trophic levels including top parts of food chains. They are widespread, diverse, and mobile, and they are sensitive to anthropogenic changes over short time-scales (GREGORY & VAN STRIEN 2010). There have been various approaches to select indicator species among birds. First, rare species may be disproportionately vulnerable to extinction and have thus dominated lists of species of conservation priority (GASTON 2008). In Europe, however, common birds are currently declining more rapidly than rare species (INGER et al. 2015), and population sizes of common species may be important indicators of the overall quality of the habitats in which they occur (Gaston 2008). Therefore, from the conservation perspective, not rarity alone should be considered but, in addition, the threat situation in which we find common species. Second, along a generalist-specialist gradient (Julliard et al. 2006), specialist species restricted to a relatively narrow ecological niche are often regarded as better indicators (Gregory & van Strien 2010). Nevertheless, again, from the conservation perspective, bird species specialised in a certain habitat type may be of least concern if the abundance and distribution of the habitat type remains stable. Availability of sites within the respective niche seems then to be more important than niche breadth (Gregory & Gaston 2000). As fine-scale mosaics of open habitats and different successional stages have become rare resources outside of protected areas and MTAs (Stoate et al. 2009, Eggers et al. 2010), we therefore assume that they represent habitats suitable for threatened species.

In Germany, comprehensive management strategies for maintaining the high level of biodiversity values on decommissioned MTAs that were transferred to the national natural heritage scheme are still missing (Ellwanger & Reiter 2019), although land owners make great efforts to manage open habitats. This is particularly true for threatened bird species that often depend not only on a specific habitat type but on the availability of multiple resources in a mosaic of habitats. The composition of habitat types in a landscape (complexity) and the physiognomic or spatial arrangement of those habitats (configuration) are two essential features required to describe any landscape (Dunning et al. 1992). From the perspective of our target bird species (organism-centred), we might define landscape as an area of land containing a mosaic of habitat patches, within which a particular "focal" habitat or resource patch is embedded (Dunning et al. 1992, McGarigal 2015). Because suitable habitat or resource patches can only be defined relative to a particular bird's perception and scaling of the environment (Wiens 1976), landscape size would differ among organisms. Accordingly, we may examine landscapes from two perspectives: First, if the territory actually occupied by a breeding bird is known, the mosaic of habitat or resource patches within the organism's normal home range can be inspected (hereafter: territory-based landscape analysis). Second, for identifying the parts of a landscape that might be occupied by the target species or species assemblage (habitat guild), the overall distribution of the suitable mosaic of habitat or resource patches may be investigated in comparison to the matrix of the (non-suitable) surroundings in a study area (hereafter: regional-scale landscape analysis). We are not aware of any study that comparatively quantified the resources required by target breeding bird species in order to derive conservation management recommendations.

Within the framework of management planning in national natural heritage areas we collected an extensive dataset containing assessments of habitats, forest structure, and breeding birds in a network of 14 decommissioned MTAs comprising in total more than 200 km² distributed all over Germany. By systematically evaluating current bird distribution patterns in relation to the complex landscapes and reviewing appropriate measures, we aimed at defining explicit quantitative goals for conserving biodiversity, as Gaston et al. (2008) identified the lack of such quantitative goals as major shortfall in the implementation of European protected area systems. Here, we specifically present our results on semi-open habitats and the related bird assemblages. Our first goal was to quantify the present-day spatial mosaic of habitat patches in our study areas. We expected that (1) decommissioned MTAs possess a significant portion of fine-scale landscape patterns, and that (2) these fine-scale patterns occur as large semi-open transition zones between open land and forests being mainly created by different stages of succession. Our second goal was to evaluate the occurrence of the target birds of semi-open habitats. Since present-day bird diversity loss in Europe is particularly high in open habitats rather than in forests (GERLACH et al. 2019, GREGORY et al. 2019), we assumed that (3) it is mainly the fine-scale semi-open mosaic of nutrient-poor open habitats and early successional stages that harbour a substantial portion of threatened bird species. Given that each bird species is (more or less) confined to the availability of certain resources, we further expected that (4) the species of the semi-open landscape bird assemblages occupy species-specific habitat resources, which can be qualified and quantified. This enabled us to provide management recommendations for six keystone bird species of the semi-open landscape guild.

2. Methods

2.1 Study areas

Our 14 study areas in Germany represent a wide range of ecosystems from the North Sea coast to the Baltic Sea islands and adjacent mainland, from the central parts to the southern fringes of the Pleistocene lowlands of eastern Germany, and to the Mesozoic scarplands and Franconian basin of northern Bavaria (Fig. 1, Table 1). Across 585 km between the most distant sites, they span large gradients in continentality and precipitation from the sub-oceanic northwest to the most sub-continental east in the far southeast of the lowlands as well as in central Bavaria. All study areas are part of the national natural heritage scheme (REITER & DOERPINGHAUS 2015). Since 2009, the formerly government-owned land was transferred to private property of the German Federal Environmental Foundation. The study areas are former MTAs that were decommissioned between 1992 and 2007. They show recurrent landscape patterns of forests that served as buffer or safety zones around military activities, which took place on one central and/or several interspersed open areas used as shooting or bombing ranges, combat zones, detonation sites, etc. These activities, often with irregular frequency, led to the conservation of open habitats such as heathlands or high nature value grasslands and to dynamic landscapes with different successional stages. Inventories comprised 20,101 ha with size of study areas ranging from 196 to 3,881 ha (mean of 1,436 ha ± 1,134 SD). In total, 49% of them are Special Protected Areas (SPA) under the European Birds Directive (2009/147/EG, and 2013/17/EU), being partly or completely classified as Important Bird Areas (IBA; DOER et al. 2002).

2.2 Habitat data

Habitats, defined as areas with particular environmental conditions that are sufficiently uniform to support a characteristic assemblage of organisms (DAVIES et al. 2004), were surveyed by using a standardised mapping protocol. This required a full survey of all habitats in a study area with the designation of vegetation types, estimated abundances of vascular plant species, and supplementary data such as structural and ecological characteristics (e.g., shrub encroachment) on the single habitat (polygon) level. Mapping scale was 1:2,500. Minimum areas for the delimitation of habitat boundaries generally applied were 0.5 ha for forest habitats and 0.1 ha for open vegetation habitats and therein dispersed single forest patches. Smaller, vegetation type-specific minimum areas of 0−1000 m² were employed for habitats protected under §30 of the Federal Nature Conservation Act (BNATSCHG 2009), which are further specified in the available guidelines of the German federal state authorities (e.g., 100 m² for heathlands). Habitats sized below the specific minimum areas were recorded as integral parts of other delimited habitats (preferably unprotected) resulting in a habitat complex with a first-order main habitat, followed by secondary-, tertiary-order etc. habitats (e.g., single trees, pathways < 5 m width, bush-grass fallow < 0.1 ha). Such subsidiary vegetation types were quantified as percentage share of the habitat complex. Habitat classification primarily followed the classification systems of the concerned

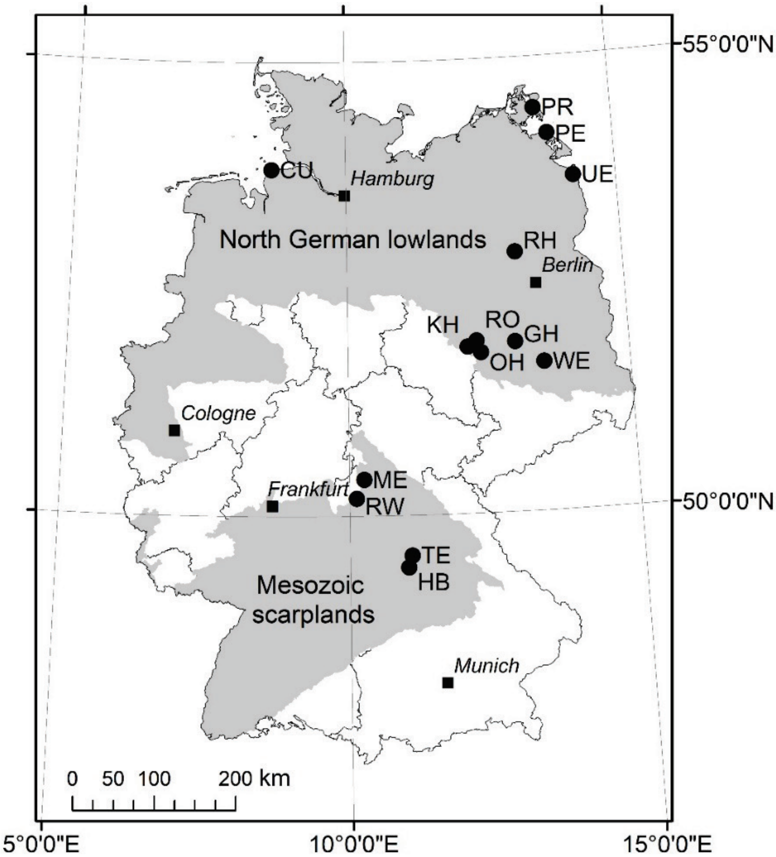

Fig. 1. Location of the study areas in the North German lowlands and the Mesozoic scarplands, Germany. The map is projected on Universal Transverse Mercator (UTM) zone 32 N, ETRS 1989. Geographical boundaries of main natural landscapes are adopted from GAUER & ALDINGER (2005) and are based on digital data made available by Thünen Institute (Braunschweig, Germany). Compare Table 1 for study area acronyms.

Abb. 1. Lage der Untersuchungsgebiete im Norddeutschen Tiefland und im mesozoischen Schichtstufenland Deutschlands. Die Karte ist in Zone 32 N, Universal Transverse Mercator (UTM), ETRS 1989, projiziert. Die Abgrenzungen der Naturlandschaften wurden von GAUER & ALDINGER (2005) übernommen und basieren auf digitalen Daten, die vom Thünen-Institut (Braunschweig, Deutschland) zur Verfügung gestellt wurden. Vgl. Tabelle 1 für Akronyme der Untersuchungsgebiete.

federal states. The primary habitat code was then translated to the best possible resolution of the standardised federal habitat code (long code; FINCK et al. 2017). Habitat surveys were conducted by specialised consultant offices from 2012−2016 taking one to two vegetation periods depending on the size of the study area (Table 1). The resulting thematic datasets were entered in a comprehensive database and combined to a non-overlapping polygon feature layer.

In the present study, we added two types of additional attributes to the thematic habitat feature dataset. First, woody plant coverage (estimated percentage cover of trees and shrubs, hereafter: wood cover) was determined for each habitat (polygon). In open habitats, wood cover was derived from the structural attribute ‘shrub encroachment’ appraised during field survey, and the percentage share of scrubs, single trees, and groups of trees as subsidiary habitats in habitat complexes. Scrubs, hedges and single forest patches imbedded in open land were estimated having 100% wood cover unless they

Table 1. Basic data on the 14 study areas within the national natural heritage scheme of Germany, located in several different federal states and main geographical landscapes, with the year in which the military training area (MTA) was decommissioned, the area of habitat and breeding bird surveys conducted between 2012 and 2018, and the corresponding number of 1 ha landscape units (LU). Climate data (mean annual temperature and rainfall) from German National Meteorological Service (DWD), based on the reference period 1981–2010, and Ivanov continentality index (K_I), derived from this data.

Tabelle 1. Grunddaten zu 14 Untersuchungsgebieten des Nationalen Naturerbes in verschiedenen Bundesländern und Hauptlandschaftseinheiten, Jahr der Stilllegung der militärischen Übungsplätze (MTA), Jahres- und Flächenangaben der Biotoptypen- und Brutvogelkartierungen mit entsprechender Anzahl von 1 ha Landschaftseinheiten (LU). Klimadaten (mittlere Jahrestemperatur und Niederschlag) des Deutschen Wetterdienstes (DWD), basierend auf dem Referenzzeitraum 1981–2010, und daraus abgeleiteter Ivanov-Kontinentalitätsindex (K_I).

	Study area	Acronym	State	Geographical landscape	MTA decommissioned (yr)	Survey area (ha)	LU (*n*)	Habitat survey (yr)	Bird survey (yr)	T_{mean} (°C)	Rainfall (mm yr^{-1})	K_I
1	Cuxhavener Küstenheiden	CU	Lower Saxony	Pleistocene lowlands	2004	1,433	1,575	2014	2015	9.4	862	75
2	Prora	PR	Mecklenburg Western Pomerania	Pleistocene lowlands	1990	1,768	2,028	2012–2013	2014	8.7	656	80
3	Peenemünde	PE	Mecklenburg Western Pomerania	Pleistocene lowlands	1996	2,027	2,312	2014–2015	2016	8.7	594	83
4	Ueckermünder Heide	UE	Mecklenburg Western Pomerania	Pleistocene lowlands	1994–2007	2,657	3,370	2013–2015	2017	8.9	571	87
5	Rüthnicker Heide	RH	Brandenburg	Pleistocene lowlands	1990	3,881	4,126	2013	2017	9.2	582	90
6	Roßlauer Elbauen	RO	Saxony-Anhalt	Pleistocene lowlands	2006	321	438	2015	2016	9.6	600	92
7	Kühnauer Heide	KH	Saxony-Anhalt	Pleistocene lowlands	1992	958	1,028	2013–2014	2015	9.8	546	92
8	Oranienbaumer Heide	OH	Saxony-Anhalt	Pleistocene lowlands	1992	2,117	2,263	2012–2013	2018	9.8	587	92
9	Glücksburger Heide	GH	Saxony-Anhalt	Pleistocene lowlands	1992	2,644	2,817	2014	2016	9.4	561	95
10	Weißhaus	WE	Brandenburg	Pleistocene lowlands	2007	1,134	1,259	2014	2017	9.2	609	94
11	Mellrichstadt	ME	Bavaria	Mesozoic scarplands	2006	207	245	2015–2016	2018	8.3	718	93
12	Reiterswiesen	RW	Bavaria	Mesozoic scarplands	1993	321	392	2015	2018	8.7	771	94
13	Tennenlohe	TE	Bavaria	Mesozoic scarplands	1994	437	506	2016	2018	9.0	777	99
14	Hainberg	HB	Bavaria	Mesozoic scarplands	1994	196	240	2016	2018	9.1	664	99

appeared in a habitat complex with subsidiary open habitat types. The estimates of wood cover in forests were based on the stocking level of contemporary forest inventory data. Second, universally valid habitat types were assigned based on the hierarchical system of the standardised federal habitat classification. Having the federal code already resolved to the long code, we assigned each habitat (polygon) to a two-digit superordinate short code on the rank of a plant community formation according to FINCK et al. (2017). Formation is a high-ranking classification level aggregating plant communities with similar plant growth forms and structural features but different species compositions (e.g., grasslands, heathlands, mires, scrubs, forests).

2.3 Bird data

Breeding birds were recorded in the entire study areas using territory mapping according to the methodological standard of SÜDBECK et al. (2005). During the breeding season (March–June/July) of the respective survey year (Table 1), each study area was visited seven times between sunrise and 10 a.m., and additionally, in order to record nocturnal species like owls or European Nightjar (*Caprimulgus europaeus*), five times between dusk and late night (each up to three times in the early and late breeding seasons). Study areas larger than 500 ha were divided into counting plots that could each be visited within one field-survey day by the investigator. During the visits, birds were recorded and classified according to the European Ornithological Atlas Committee (EOAC) criteria as applied in the Atlas of European breeding birds (HAGEMEIJER & BLAIR 1997) that distinguishes between "possible breeding" ('A'), "probable breeding" ('B'), and "confirmed breeding" ('C') categories. In this study, "breeding" in terms of breeding pair and "territory" in terms of individual territorial behaviour even without confirmed breeding record are used synonymously. A "territory" was defined as (1) any two records of species-specific territorial behaviour on separate days at a minimum seven-day interval during the main breeding season of each species (category 'B'), or (2) single records of evident breeding activity (e.g., observation of nests with eggs or chicks or food-carrying adults, category 'C'). The survey included all bird species native to and regularly breeding in Germany that are considered being rare (annually up 10,000 pairs/territories) or semi-frequent (>10,000−100,000) (GRÜNEBERG et al. 2015). Common bird species (> 100,000) were only recorded if they were listed in Annex I of the European Birds Directive, red-listed in Germany (GRÜNEBERG et al. 2015) or protected under the Federal Nature Conservation Act (BNATSCHG 2009). Yellowhammer (*Emberiza citrinella*), Common Redstart (*Phoenicurus phoenicurus*), and Common Starling (*Sturnus vulgaris*), all common bird species of least concern according to the 4th ed. of the German red list of birds (SÜDBECK et al. 2007), were moved to 'near threatened' in the 5th ed. (GRÜNEBERG et al. 2015), thus these species were not considered in the survey of 2014. Bird surveys were conducted by specialised consultant offices from 2014−2018. The resulting thematic datasets (bird territory centroids) are available as an attributed point feature layer. Unique species codes were given following the European Union for Bird Ringing species code (EURING 2019). Nomenclature of scientific and English bird names follows GILL & DONSKER (2019).

In this study, we only evaluated records of probable and confirmed breeding bird territories (EOAC categories 'B' and 'C'), which were situated with their territory's centroid in the extent of the available habitat maps. This applied to a total of 93 bird species. We assigned these species to habitat guilds and identified the home ranges (mean territory areas) of the bird species related to semi-open landscapes in Central Europe based on an extensive literature research (FLADE 1994, GLUTZ VON BLOTZHEIM & BAUER 1998, BAUER et al. 2005). The analysis across habitat-specific guilds included all breeding bird species recorded under the above-mentioned selection criteria, but neglected the colony-breeding Great Cormorant (*Phalacrocorax carbo*), because it occupied only few hectares (< 0.05% of the study areas).

2.4 Landscape-scale data compilation

We analysed the landscapes of the study areas on two spatial scales, following the two approaches referred to in chapter 1, the regional scale defined as the entire study area (regional-scale landscape analysis) and the territories occupied by breeding birds as sections of the landscape (territory-based landscape analysis).

For the regional-scale landscape analysis, we subdivided each of the 14 study areas into 1 ha (100 × 100 m) grid-cells (hereafter: landscape units) by using the Grid Index Features tool integrated in the Cartography toolbox of ArcGIS Desktop Advanced applications v. 10.5.1 (ESRI Inc., Redlands, CA), starting in the most north-western corner and filling the rows consecutively to the study area borderline. This grain size is close to the average (median) range of the territories of 1.5 ha typically occupied by the studied bird species of semi-open landscapes during the breeding season. According to the habitat mapping scheme, 1 ha is furthermore amply above the minimum area of 0.1 ha for the delimitation of isolated forest habitat patches. This allowed us identifying our target habitats that were semi-open landscapes with transitional habitat complexes (ecotones), where a mosaic of predominating open vegetation patches was intermingled with forest patches.

We computed a geometric union of the polygon feature datasets of landscape units and habitats and wrote all features and their attributes to a unified output feature class (union function). Based on this unified dataset we calculated several aggregated structural and compositional attributes and wrote them to the landscape unit feature dataset. To avoid edge effects in landscape units that had incomplete habitat data because they were situated at the borderline of a study area, we added the total habitat area per landscape unit to be considered as reference area in the subsequent analyses. We summarised the wood cover (in %) of each landscape unit as the average of the area-weighted wood cover of all occurring habitats. In total, we used 22,599 landscape units covering 20,101 ha of survey area.

Territory-based landscape analysis was performed on the section of the landscape that represented the normal home range of the breeding birds. We compiled the information on species-specific mean home range areas during the breeding season from literature (Supplement S1). Estimating relatively even mobility patterns of breeding birds we generated circular polygons centred on the input points of territory centres using the buffer function of the ArcGIS Analysis toolbox. We computed a geometric union of the polygon feature datasets of bird territories for each species and habitat and wrote all features and their attributes to a unified output feature class (union function) and deleted all outlying spatial information. For each single bird territory, we then calculated wood cover and formation shares using the same procedures as described for the landscape units. In total, the number of territories accounted for in this study was 3,125 covering 3,754 ha of habitat area (after the union of overlapping territories).

To account for the explanatory value of the climatic conditions in the study areas, we used temperature and precipitation data available as interpolated 100 ha raster datasets for the period 1981−2010 (DWD 2019). For each landscape unit and territory, we extracted the mean annual temperature and precipitation values from the centre of the closest climate data grid cell. Furthermore, we calculated the Ivanov continentality index K_I (FRANKENBERG 1991), which is based on temperature values and geographical latitude, with values $K_I < 100$ indicating an oceanic climate and $K_I > 100$ continental climate.

2.5 Statistical analysis

Statistical analysis was performed using RStudio v. 1.2.1335 (RSTUDIO TEAM 2019, based on R v. 3.6.2, R CORE TEAM 2019), unless otherwise stated.

Landscapes were classified based on wood cover values of the 1 ha landscape units into five clusters using the 'kmeans' algorithm implemented in the 'classIntervals' function of the 'classInt' package (VIVAND et al. 2019) (Table 2, Fig. 2). The *k*-means algorithm clusters similar objects into a predefined number of clusters in which each observation belongs to the cluster with the nearest mean, preferring clusters with low variance and similar size (MACKAY 2005). To evaluate the spatial association of landscape units (cluster and outlier analysis), Anselin Local Moran's I (ANSELIN 1995) based on wood cover values was calculated, with the 'inverse distance' and the 'Euclidean distance' options and 499 random permutations for estimating pseudo *p*-values ($p \leq 0.05$), by using the Mapping Clusters tool integrated in the Spatial Statistics toolbox of ArcGIS.

Out of the observed breeding bird species of semi-open landscapes, a subset of six keystone species was selected representing different abundances across the dataset and a range of intermediate-sized bird territories. We excluded species when they had (1) territories > 3 ha in order to avoid edge effects (missing landscape data), (2) small total sample sizes (< 30 breeding pairs/territories), (3) a high estimated proportion of missing data (semi-frequent birds that were red-listed only in 2015), or were (4) host- or colony-breeding. The remaining subset covered the large majority (79%) of the sample total. Differences in species-attributed wood cover values in territories (as the dependent variable) were analysed using linear mixed effects models (LME) that incorporate both fixed- and random-effects terms in a linear predictor expression from which the conditional mean of the response can be evaluated (BATES et al. 2015) (Fig. 4, Supplement E2). We created and tested the fit of five different models against a null model by using 'lmerTest' package (KUZNETSOVA et al. 2019), which integrates the 'lmer4' package (BATES et al., 2019). Wood cover was square root-transformed in order to best approach a normal distribution. To account for the block structure of the study areas, we used the study area as random-effects term of the form (1 | *studyarea*) in all fitted models, and in the null model the alternative term 1 + (1 | *studyarea*), meaning a random intercept with fixed mean. As fixed effects we used the scaled (z-transformed) K_I and the scaled geographical latitude (x_coord) (as independent variables) in different combinations as factors and interactions with species. Models were tested with t-tests using Satterthwaite's method. ANOVA-based comparison of all models resulted in the best fitting model formula:

$$model \leftarrow lme(woodcov_{sqrtrans} \sim species * scale(K_I) + scale(x_{coord}) + (1 \mid studyarea))$$

Habitat types that differentiated the territories of the different bird species were identified by the algorithm proposed by TSIRIPIDIS et al. (2009), which uses a fidelity threshold based on differences in relative constancy (Table 3). Here, 'fidelity' measures the association of certain bird species with a habitat class. The algorithm searches for habitats, which in one or more groups are positively or negatively differentiated against one or more other groups. The phi coefficient (φ) is the most appropriate fidelity measure if dataset sizes vary (CHYTRÝ et al. 2002), because the influence of the total number of samples in a dataset as well as that of the relative number of samples in the compared bird species is reduced by standardisation procedures. Positive/negative values of φ, which may take values from -1 to +1, indicate that the habitat type occurs more/less frequently than would be expected by chance. We calculated fidelity measures by using a macro incorporated in a MS Excel (Microsoft Corp., Redlands, CA) spread sheet.

3. Results

3.1 Structural configuration of landscapes

Structural classification of landscape units resulted in five natural wood cover classes (Fig. 2a–b, Table 2, Supplement E1). A total of 22,599 landscape units, sized 1 ha, covered a survey area of 20,101 ha. Accounting for landscape units situated at the border of a study area, we found an even distribution of incompletely surveyed landscape units across the classes (mean count : area ratio between classes = 1.1 ± 0.1 sd).

Wood-dominated landscapes with ≥ 68% wood cover (c4) and closed forests with ≥ 87% wood cover (c5) together made up for about 60% or c. 12,126 ha of the total survey area. Semi-open landscapes occurred in two distinct wood cover classes (c2, c3), summing up to about 5,548 ha or less than a third (28%) of the survey area (mean 33% ± 15 sd). Thereof, sparsely wooded semi-open landscapes (c2) contained scattered trees and shrubs that covered between 20 and 46% of a landscape unit. They differed from densely wooded semi-open landscapes (c3) with scattered or clustered trees and shrubs with ≥ 46 to 68% wood cover. In most study areas, densely wooded semi-open landscapes with an average share of 18% (± 7 sd) were slightly higher represented than sparsely wooded semi-open landscapes

Fig. 2. Classification of 1 ha landscape units (n = 22,599) based on percentage wood cover. (a) Histogram of wood cover values in 5% intervals and a normal curve with the mean of 65.9% (± 31.0 sd). (b) Class intervals of five clusters with break values generated by the *k*-means algorithm. (c) Differences in spatial association based on z-scores of Anselin Local Moran's I between wood cover classes c1–c5 derived from *k*-means analysis with 0.95 confidence level (dashed horizontal lines), z-scores ≥ 1.96 meaning that neighbouring landscape units have significantly similar low or high cover values (spatial clustering) and z-scores ≤ -1.96 meaning that a landscape unit is an outlier having a significantly higher or lower cover value than the neighbouring landscape units. Boxes are drawn with widths proportional to the square-roots of the number of observations in the groups. Notches show that medians of all groups are significantly different at $p \leq 0.05$.

Abb. 2. Klassifizierung von 1 ha Landschaftseinheiten (n = 22.599) anhand der prozentualen Gehölzbedeckung. (a) Histogramm der Gehölzbedeckungswerte in Intervallen von 5 % und eine Normalverteilungskurve mit einem Mittelwert von 65,9 % (± 31,0 sd). (b) Klassenintervalle von fünf Clustern mit vom *k*-Mittelwert-Algorithmus erzeugten Unterbrechungswerten. (c) Unterschiede in der räumlichen Klumpung, basierend auf den Z-Scores des Anselin Local Morans I zwischen den Gehölzbedeckungsklassen c1–c5, abgeleitet aus der *K*-Mittelwert-Analyse mit einem Konfidenzniveau von 0,95 (gestrichelte horizontale Linien). Z-Scores ≥ 1,96 bedeuten, dass benachbarte Landschaftseinheiten signifikant ähnliche niedrige oder hohe Deckungswerte besitzen (räumliche Clusterbildung) und Z-Scores ≤ -1,96 bedeuten, dass eine Landschaftseinheit ein Ausreißer mit einem signifikant höheren oder niedrigeren Deckungswert als die benachbarten Landschaftseinheiten ist. Die Breite der Boxplots ist proportional zur Quadratwurzel der Anzahl der Beobachtungen in der jeweiligen Gruppe. Einkerbungen zeigen an, dass die Mediane aller Gruppen bei $p \leq 0,05$ signifikant unterschiedlich sind.

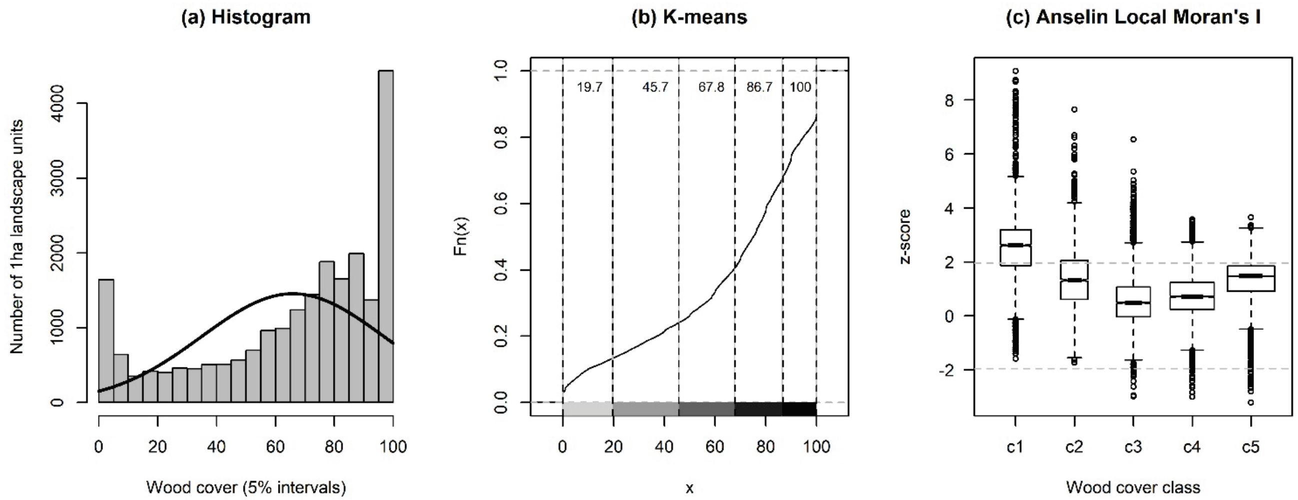

Table 2. Description of five structural landscape types based on wood cover classes (c1−c5) with upper thresholds of percentage wood cover in 1 ha landscape units (LU), the respective habitat area (ha), and the proportion of landscape based on the total habitat area of all study areas and the mean proportion of landscapes (± sd, in %) in 14 national natural heritage areas in Germany. Compare Supplement E1 for study area details.

Tabelle 2. Beschreibung der fünf strukturellen Landschaftstypen nach Gehölzbedeckungsklassen (c1-c5) mit oberen Schwellenwerten für die prozentuale Gehölzbedeckung in 1 ha Landschaftseinheiten (LU), der jeweils kartierten Biotopfläche (ha), dem Anteil an der Gesamtlandschaft (basierend auf der gesamten Fläche aller Untersuchungsgebiete) und dem mittleren Anteil an der Landschaft (± Standardabweichung, in %) auf 14 Naturerbeflächen. Vgl. Anhang E1 für Details zu den Untersuchungsgebieten.

Class	Wood cover (%) upper threshold	Description	LU (*n*)	Habitat area (ha)	Proportion of landscape, total (%)	Proportion of landscapes, mean ± sd (%)
c1	19.7	Open landscape (at most few single/isolated trees/shrubs)	3,018	2,427	12.1	16.4 ± 13.5
c2	45.7	Sparsely wooded semi-open landscape (trees/shrubs scattered)	2,435	2,188	10.9	14.7± 8.2
c3	67.8	Densely wooded semi-open landscape (trees/shrubs scattered to clustered)	3,712	3,360	16.7	18.1 ± 7.3
c4	86.7	Wood-dominated landscape	6,234	5,737	28.5	27.0 ± 11.3
c5	100.0	Landscape with closed wood canopy/closed forests	7,200	6,390	31.8	23.7 ± 17.1
Sum			22,599	20,101	100.0	

(mean 15% ± 8 sd). Absolute semi-open area (c2+c3) per study area varied widely from 77 ha to 1,251 ha (in mean 396 ha ± 345 sd). We identified the largest semi-open areas in the north-eastern German Pleistocene lowlands (study areas GK, PR, OH, and UE). The six smaller study areas (< 1,000 ha) had a higher proportion of semi-open area (mean 42%) than the other eight study areas (mean 26%).

The two types of semi-open landscapes (c2, c3), wood-dominated landscapes (c4) and landscapes with closed wood canopy (c5) formed large-scale coherent ecotones (Fig. 2c). Such smooth transitions between landscapes with different wood cover values were indicated by Anselin Local Moran's I analysis that showed, with the interquartile range of boxplots of z-scores between + 1.96 and -1.96, a distribution as random mosaics in 50% or more of all landscape units in wood cover classes c2−c5. However, medians of all groups were significantly different and sparsely wooded semi-open landscapes (c2) and closed forests (c5) tended to cluster. This contrasted to the configuration of open landscapes (c1), which showed distinctive spatial structuring. In total, they constituted only 12% (mean 16% ± 14 sd) of the study areas, but more than 50% of them were significantly more clustered than expected by chance.

3.2 Abundances of habitat-specific guilds

We counted a total of 6,476 breeding pairs or territories of 93 bird species across all habitat-specific guilds (Fig. 3). Nearly half of the pairs/territories (*n* = 3,047 or 47%) represented 'threatened' bird species (national red list categories RL1−RL3), and another 30% (*n* = 1,963) were classified 'near threatened' (NT). The bird guild associated with semi-open landscapes was exceptionally large accounting for 61% (*n* = 3,937) of the total and 71% (*n* = 2,152) of all bird species classified 'threatened'. Among the threatened birds, the guild of open landscapes was the second-largest group (*n* = 964 in all, *n* = 645 in RL1−RL3 species), with Eurasian Skylark (*Alauda arvensis*), European Stonechat (*Saxicola rubicola*), Whinchat (*Saxicola rubetra*), and Corn Bunting (*Emberiza calandra*) being the most abundant species (89% of the guild total). Despite the large forested area (Table 2), the forest-specific guild was relatively small (*n* = 962) and its species were largely of 'least concern' (LC) or 'near threatened' (NT).

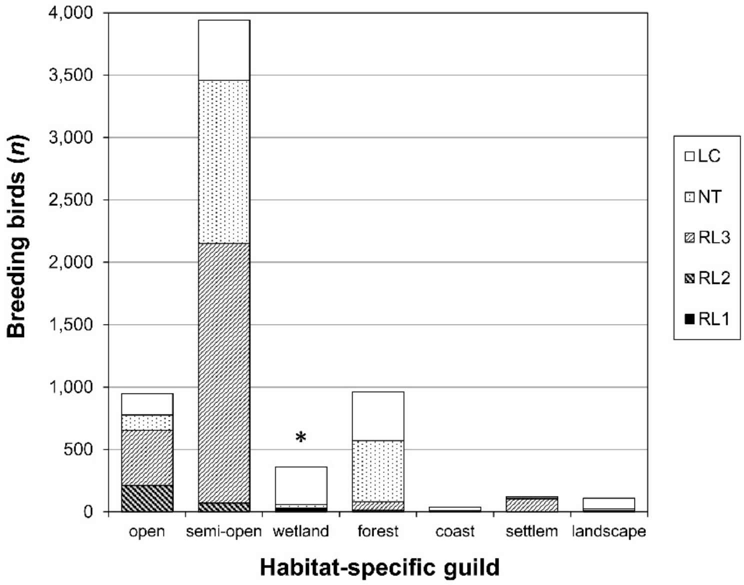

Fig. 3. Breeding birds with probable or confirmed breeding (based on EOAC categories 'B' or 'C') sorted by habitat-specific guilds in 14 national natural heritage areas in Germany. Different signatures indicate the status according to the German Red List of breeding birds (GRÜNEBERG et al. 2015), with the threat categories 'RL1' (critically endangered), 'RL2' (endangered), and 'RL3' (vulnerable), and, furthermore, 'NT' (near threatened) for species added to the pre-warning list, and 'LC' (least concern) for unthreatened species. A total number of 6,476 breeding birds were counted in 92 species, and, as indicated by the asterisk, an additional 4,071 colony-breeding Great Cormorants (*Phalacrocorax carbo*) were recorded at Peenemünde (PE).

Abb. 3. Brutvögel mit wahrscheinlicher oder bestätigter Brut (basierend auf den EOAC-Kategorien „B" oder „C"), sortiert nach lebensraumspezifischen Gilden auf 14 Naturerbeflächen. Unterschiedliche Signaturen geben den Status gemäß der Roten Liste der Brutvögel Deutschlands (GRÜNEBERG et al. 2015) mit den Gefährdungskategorien 'RL1' (vom Aussterben bedroht), 'RL2' (stark gefährdet) und 'RL3' (gefährdet) an. Zusätzliche Kategorien sind "NT" (Vorwarnliste) und "LC" (ungefährdet). Insgesamt wurden 6.476 Brutvögel aus 92 Arten gezählt. Das Sternchen zeigt an, dass in Peenemünde (PE) zusätzlich 4.071 Kormorane (*Phalacrocorax carbo*) gezählt wurden.

3.3 Diversity and distribution of birds of semi-open landscapes

We recorded 20 bird species associated with semi-open landscapes with a total of 3,937 records of probable or confirmed breeding status (Supplement S1). Tree Pipit (*Anthus trivialis*) was most abundant comprising 1,586 or 40% of all territories. Further common species that were present in almost all study areas, each with a total of > 300 territories, were Yellowhammer, Woodlark (*Lullula arborea*), and Red-backed Shrike (*Lanius collurio*). An additional eight species were similarly distributed across all study areas but had lower frequencies. Among them, the European Nightjar was restricted to areas dominated by dry sandy soils. It was most frequent in the subcontinental north-eastern lowlands, in particular in the study areas OH and GH, which represented exceptionally large semi-open landscapes. Similar distribution patterns, even more restricted to the north-eastern lowlands, were found in Great Grey Shrike (*Lanius excubitor*) and Eurasian Hoopoe (*Upupa epops*), which both possess very spacious home ranges of 40 and 70 ha, respectively. Barred Warbler (*Sylvia nisoria*) had its main distribution centre in the study areas close to the Baltic Sea (PR, PE), but reached as far as the south-eastern border of the north-east German lowlands. Other rare birds centred to our study areas at the Baltic Sea shoreline of Mecklenburg Western Pomerania (PR, PE, UE) were Common Rosefinch (*Carpodacus erythrinus*), River Warbler (*Locustella fluviatilis*), and Thrush Nightingale (*Luscinia luscinia*). Considering the semi-open landscapes identified in the study areas (wood cover classes c2+c3) as suitable habitats, we estimated an average bird density of 0.7 breeding pairs or territories ha^{-1}. Highest densities of 2.4 and 1.6 birds ha^{-1} were recorded in semi-open limestone areas of Bavaria (RW, ME).

3.4 Bird species-specific habitat occupation

Characteristic birds of semi-open landscapes occupied different species-specific structural habitats (Fig. 4). Mean wood cover values in territories varied significantly between all six selected species (LME: $p \leq 0.01$, Supplement E2). The territories occupied by these bird species were composed of a high number of co-occurring habitat types and showed distinct compounds characterising specific niches (Table 3, Fig. 5).

Tree Pipit, the most frequent species, was associated with densely wooded habitats (c3), with a specific mean wood cover of 58% and the widest wood cover range (interquartile range, IQR: 33−83%). It was closely associated with coniferous forests occurring with a mean percentage cover of 45% in its territories correlating with the described relatively high wood cover values that distinguished it from all other investigated species. An overlapping niche was occupied by Red-backed Shrike and Barred Warbler, which concentrated in transition zones from open (c1) to sparsely wooded semi-open (c2) landscapes and had an upper limit (0.75p) at about 34 and 32% wood cover, respectively. Both species were highly dependent on the presence of shrubs and hedges. The rare Barred Warbler was almost exclusively distributed in study areas with maritime climatic conditions (Supplement S1: PR, PE; Supplement E2: LME: species*K_I interaction, $p \leq 0.05$), and showed the most complex habitat dependency being strongly associated to grasslands, salt meadows and other open coastal habitats at its distribution peak in PE, as well as wetlands and reeds, but also broad-leaved forests. The relatively frequent Red-backed Shrike also showed a peak associated with maritime climate (PR, PE) and a secondary peak in KH and OH but appeared with varying numbers in all study areas (Supplement S1).

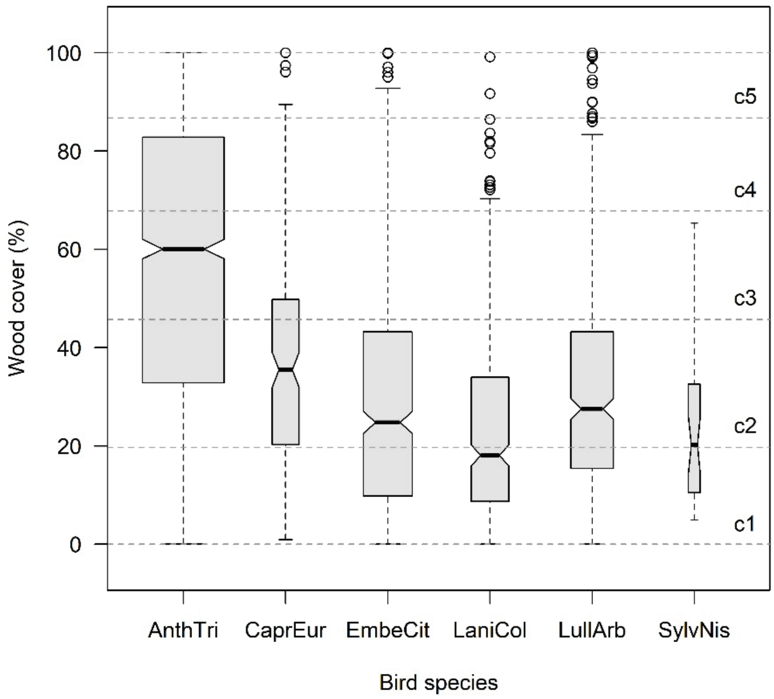

Fig. 4. Structural characteristics of habitats by means of wood cover (in %) in the territorial ranges of six breeding bird species of semi-open landscapes (*n* = 3,125) in 14 national natural heritage areas in Germany. Compare Supplement S1 for full scientific bird species names and Supplement E2 for statistical results. Boxes are drawn with widths proportional to the square-roots of the number of observations in the groups, and notches display the 95% confidence interval of the median. Dashed horizontal lines depict thresholds of wood cover classes (c1−c5).

Abb. 4. Strukturelle Merkmale der Lebensräume von sechs Brutvogelarten halboffener Landschaften auf Grundlage der Gehölzbedeckung (in %) in Revieren (*n* = 3.125) auf 14 Naturerbeflächen. Vgl. Beilage S1 für vollständige wissenschaftliche Vogelartnamen und Anhang E2 für weitere statistische Analyseergebnisse. Die Breite der Boxplots ist proportional zu den Quadratwurzeln der Anzahl der Beobachtungen in den Gruppen, Einkerbungen zeigen das 95 % -Konfidenzintervall des Medians an. Gestrichelte horizontale Linien zeigen Schwellenwerte der Gehölzbedeckungsklassen an (c1–c5).

The focal structural habitats of European Nightjar, Yellowhammer and Woodlark were sparsely wooded semi-open landscapes (c2). European Nightjar, which is a semi-frequent species, extended into densely wooded landscapes (0.75p = 50% wood cover) but did not overlap with open landscapes. It lived at forest fringes in a complex with heathlands that reached high cover values of 52% on average, but avoided a high coverage of coniferous as well as broadleaved forests. Woodlark and Yellowhammer, both frequent species, did not extend into densely wooded but to open landscapes (0.25p = 10 or 15% wood cover). Woodlark was highly associated with heathlands, although grasslands were present with on average 27% coverage and a substantial population on Bavarian calcareous dry grasslands (ME, RW, cp. Supplement S1). Yellowhammer was the only species that showed no distinct habitat type preferences, also it tended to avoid heathlands and forest fringes.

Table 3. Mean percentage cover of habitat types (F08–F57, according to FINCK et al. 2017) in territories of six selected breeding bird species of semi-open landscapes in 14 national natural heritage areas. Habitat types that, based on constancy tables, positively differentiated the territories of the different bird species are printed in bold letters with grey-shaded fields, and those that negatively differentiated are printed solely in bold letters, with phi coefficients (φ) given for differential habitat types. Compare Supplement S1 for full scientific bird species names.

Tabelle 3. Mittlerer prozentualer Deckungsgrad der Vegetationsformationen (F08–F57, nach FINCK et al. 2017) in den Revieren sechs ausgewählter Brutvogelarten halboffener Landschaften auf 14 Naturerbeflächen. Vegetationsformationen, die auf der Grundlage von Stetigkeitstabellen die Reviere der verschiedenen Vogelarten positiv differenzierten, sind in fetten Buchstaben mit grau schattiertem Hintergrund gedruckt, und diejenigen, die negativ differenzierten, sind ausschließlich in fetten Buchstaben gedruckt, wobei der Phi-Koeffizient (φ) für differenzierende Vegetationsformationen angegeben ist. Vgl. Beilage S1 für vollständige wissenschaftliche Vogelartennamen.

FID	Habitat type	AnthTri	CaprEur	EmbeCit	LaniCol	LullArb	SylvNis	φ
	n	1,586	173	567	338	427	34	
F08	**Salt meadows**	**0.08**	**.**	**0.12**	**1.75**	**.**	**14.53**	0.50
F09	**Beach and sea shore**	**0.01**	**.**	0.01	0.05	**.**	**0.57**	0.39
F10	**Dunes**	**0.05**	**.**	**0.18**	0.38	**.**	**3.45**	0.41
F11	Cliffs	0.01	.	.	0.09	.	.	.
F22	Springs	.	.	0.01	.	0.01	.	.
F23	Flowing water	0.03	.	0.06	0.46	.	0.95	.
F24	Still water	0.05	0.20	0.03	0.32	0.18	0.54	.
F32	Rocks	0.12	0.10	0.49	0.08	0.28	.	.
F33	Fields	0.14	.	0.08	0.62	0.21	.	.
F34	**Grasslands**	**10.98**	9.14	40.38	34.09	27.40	**31.31**	0.25
F35	**Wetlands**	**0.45**	**0.06**	2.61	6.91	**0.70**	**7.75**	0.38
F36	Raised bogs	0.29	0.00	0.23	0.63	0.19	.	.
F37	Sedge fens	0.13	.	0.07	0.93	0.01	.	.
F38	**Reeds**	0.12	**.**	1.33	4.12	0.08	**3.59**	0.25
F39	Forbs and copse	7.03	10.09	11.59	13.49	12.66	9.80	.
F40	**Heathlands**	16.84	**52.38**	**11.62**	**10.54**	**30.30**	**6.00**	0.52
F41	**Shrubs and hedges**	**1.07**	**0.14**	3.75	**8.14**	1.31	**4.37**	0.33
F42	**Forest fringes**	7.50	**15.30**	**2.38**	**2.16**	8.31	5.67	0.28
F43	**Broadleaved forests**	9.26	**1.84**	10.86	6.83	3.52	**10.42**	0.23
F44	**Coniferous forests**	**44.81**	**10.46**	11.21	7.29	13.62	**0.75**	0.26
F51	Gardens	.	.	.	.	0.03	.	.
F52	Traffic	0.90	0.28	2.82	0.93	1.14	0.31	.
F53	Buildings	0.07	.	0.07	0.14	0.02	.	.
F54	Disposal sites	0.04	.	0.04	0.05	.	.	.
F57	Others	0.02	.	0.07	.	0.03	.	.

Among all selected bird species, wood cover range (IQR) varied from 50 in Tree Pipit to 21 in Barred Warbler, almost linearly descending with count numbers. Thus generally, with exception of European Nightjar (IQR = 30), the rarer a species was, the smaller was its occupied niche in terms of wood cover in its territory.


a)
b)
c)
d)
e)
f)
g)
h)

4. Discussion

Actively used MTAs are landscapes with heterogeneous disturbance regimes, in which different successional stages are present simultaneously occurring as fine-scaled mosaics (WARREN et al. 2007). Intense military exercises can be beneficial for pioneer communities of fauna and flora, followed by other successional stages (GAZENBEEK 2005). Having been decommissioned 13−30 years ago our 14 former MTAs were still very heterogeneous landscapes as shown by five distinct wood cover classes each covering significant portions of the landscapes (Fig. 2b, Table 2). While open landscapes appeared as connected open areas, semi-open landscapes, wood-dominated landscapes, and closed forests were mostly patchy mosaics merging into each other (Fig. 2c). This contrasts with the widely identified ongoing homogenisation of Central European landscapes driven by agricultural intensification,

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Fig. 5. Semi-open landscape sceneries of selected study areas: **a)** *Juniperus communis* formation on heath over flint-stone beach wall formation (Prora, August 2018); **b)** Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) with interspersed single shrubs and trees (Mellrichstadt, April 2018); **c)** Mosaic of *Calluna* heathland (*Genistion pilosae*), and xeric sand grassland (*Koelerion glaucae*), all-year grazed by cattle and horses, with *Betula pendula* succession thinned to 30% wood cover (Oranienbaumer Heide, June 2015); **d)** Marshes and salt meadows (*Glauco-Puccinellietalia maritimae*, *Thero-Salicornietea*) with scattered scrubs, extensively grazed by cattle (Peenemünde, May 2017); **e)** Inland dunes with open grasslands and dry sand heath with *Calluna* and *Genista*, and *Cytisus scoparius* scrubland, in transition to *Pinus sylvestris* forest, grazed by Przewalski horses (Tennenlohe, July 2012); **f)** Structurally rich, sparse *Pinus sylvestris* forest with *Vaccinium myrtillus* undergrowth (*Vaccinio-Pinetum*) with manifold inner forest fringes (Weißhaus, July 2016); **g)** Forest fringe with smooth transition zone from heathland to forest (Cuxhavener Küstenheiden, June 2019); **h)** Fine-scale mosaic of open heathlands (purple), *Calamagrostis* grassland (light-green), and successional trees (*Pinus sylvestris*, *Betula pendula*) (Glücksburger Heide, September 2004), contrasting to the agricultural landscape in the background (Photos: (a–g) H. Culmsee, (h) F. Meyer, Halle (Saale)).

Abb. 5. Halboffene Landschaften ausgewählter Untersuchungsgebiete: **a)** *Juniperus communis*-Formation auf Zwergstrauchheide über dem Strandwallsystem der Feuersteinfelder (Prora, August 2018); **b)** Naturnahe Kalk-Halbtrockenrasen und deren Verbuschungsstadien (*Festuco-Brometalia*) mit eingestreuten einzelnen Sträuchern und Bäumen (Mellrichstadt, April 2018); **c)** Mosaik trockener europäischer Heiden (*Genistion pilosae*) und subkontinentaler Blauschillergrasrasen (*Koelerion glaucae*) mit ganzjähriger Rinder- und Pferdebeweidung sowie *Betula pendula*-Sukzession, die auf 30 % Gehölzbedeckung reduziert wurde (Oranienbaumer Heide, Juni 2015); **d)** Von Rindern beweidete Sümpfe und Salzwiesen (*Glauco-Puccinellietalia maritimae*, *Thero-Salicornietea*) mit vereinzelten Gehölzen (Peenemünde, Mai 2017); **e)** Binnendünen mit offenen Grasflächen und trockenen Sandheiden mit *Calluna* und *Genista* sowie *Cytisus scoparius*-Gebüschen, die von Przewalski-Pferden beweidet werden, im Übergang zu Kiefern-Wald (*Pinus sylvestris*) (Tennenlohe, Juli 2012); **f)** Strukturreicher, lichtdurchfluteter Kiefern-Wald mit *Vaccinium myrtillus* (*Vaccinio-Pinetum*) mit vielfältigen Waldinnenrändern (Weißhaus, Juli 2016); **g)** Waldrand mit sanfter Übergangszone von einer offenen Heide zum geschlossenen Wald (Cuxhavener Küstenheiden, Juni 2019); **h)** Feinskaliges Mosaik aus offenen Heideflächen (lila), *Calamagrostis*-Grasland (hellgrün) und Gehölzsukzession (*Pinus sylvestris, Betula pendula*) (Glücksburger Heide, September 2004), das in starkem Kontrast zur Agrarlandschaft im Hintergrund steht (Fotos: (a–g) H. Culmsee, (h) F. Meyer, Halle (Saale)).

urbanisation, and land abandonment (SUTCLIFFE et al. 2015, BÁLDI & BATÁRY 2011, STOATE et al. 2009). However, with wood-dominated landscapes and closed forests together making up about 60% of the study areas, late successional stages largely dominated the decommissioned MTAs.

Open landscapes covered 12% of the study areas and were the only cover class that occurred significantly clustered, i.e., as continuous open land. This suggests that management measures, such as grazing or mowing, have been taken for preserving open landscapes. Being part of the national natural heritage scheme and, in addition, in most cases of the European Natura 2000 protected area system, the studied decommissioned MTAs were not completely abandoned to natural succession, but, instead, alternative management measures were implemented in at least part of the areas, such as large herbivore grazing regimes (LORENZ et al. 2016) or controlled burning (SCHULZE et al. 2015). It apparently is difficult to substitute the often-incidental disturbance dynamics of military use by other mechanical measures, because the latter are usually not as severe and often remain spatially fixed by pasture fences, leased farmland or agricultural support boundaries. In Central Europe, specific pioneer communities (e.g., pioneer grasslands on sandy soils) have largely declined in decommissioned MTAs and, although parts of these landscapes may still remain structurally open, they have been followed by other successional stages (e.g., heathlands, later grassland stages with closed vegetation cover) (ELLWANGER & REITER 2019). Management options have been developed for restoring semi-open heathland landscapes by controlled burning that creates bare soil followed by heathlands and tree succession (SCHULZE et al. 2015). An experimental study found that topsoil removal and tank driving could fully restore pioneer plant communities (JENTSCH et al. 2009), though substitution measures should be economically feasible and top soil removal is often prohibited because of contamination with munition on these sites. Nevertheless, former MTAs have low nitrogen loads and the subsequent management, which is usually extensive, is comparable to traditionally managed landscapes (BUŠEK & REIF 2017). Such open habitats are usually of high conservation value. Thus, despite the relatively small open area, our study areas harboured substantial populations of endangered bird species (Fig. 3), which are themselves dependent on mostly relatively rare and often threatened open habitat types.

A unique characteristic of our study areas were large semi-open landscapes with a total cover of 28% of the survey area. We defined semi-open landscapes as transition zones between open land and forests, in which open habitats (e.g., heathlands, semi-natural grasslands) are interlinked with scrubs, single or groups of trees. We found two distinct classes, sparsely wooded (>20–46% wood cover) and densely wooded (> 46–68%) semi-open landscapes (Table 2). Birds associated with these semi-open landscapes made up 61% of all breeding bird records and 71% of all breeding birds classified 'threatened' (Fig. 3, Supplement S1). Thus, this habitat guild is of primary conservation concern and semi-open landscapes must be regarded as extraordinary diversity hotspots and refuges for threatened birds. The high proportion of threatened birds suggests that such semi-open habitat complexes have become a rare resource in the surrounding Central European landscapes. In the context of actively used MTAs in the Czech Republic, the number of threatened bird species was significantly higher in the MTAs than in the control areas (BUŠEK & REIF 2017), and early-successional stages hosted bird communities with the highest habitat specialisation and threat level (REIF et al. 2013). Abandoned MTAs also possessed higher number of birds of conservation concern associated with open habitats than predicted by their total population size (REIF et al. 2011). Open and semi-open habitats of abandoned MTAs were identified as overlooked refuges for threatened bird species, but were in risk of forest succession (REIF et al. 2011). However, semi-open landscapes also exist as remnants of traditional land use practices (PERINGER et al. 2013). Also newly created semi-open wood pastures had higher bird species richness compared to ungrazed forests and open pastures, and more breeding pairs per area compared to open pastures (RÖSCH et al. 2019). While natural temperate forests show naturally open regeneration/establishment and terminal/decay stages, in which bird diversity is high (HILMERS et al. 2018), modern production forests that are permanently managed in the optimum phase have closed canopies that are not suitable for birds of semi-open habitats. Therefore, small clear-cuts (PAQUET et al. 2006) as well as newly created wood pastures with semi-open conditions (RÖSCH et al. 2019) have received increasing attention as nature conservation tools.

BENTON et al. (2003) identified ecological heterogeneity at multiple spatial and temporal scales as a key to restoring and sustaining biodiversity in temperate agricultural systems. We found that our six keystone species of the bird guild of semi-open habitats occupied different species-specific habitat resources (Fig. 4, Table 3). Regarding structural habitat characteristics, the optimum wood cover of each species ranged from open habitats with few structural elements to sparsely wooded and densely wooded semi-open landscapes. In southern Sweden, farmland birds, such as the Yellowhammer and the Red-backed Shrike, occupied forest clear-cuts and powerlines as alternative man-made habitats showing an optimum remaining tree cover of about 25% (BAKX et al. 2020). Although in an entirely different ecosystem setting, Australian farmland birds responded to structural landscape characteristics alike with species-specific optimum curves along gradients of tree density (HANSPACH et al. 2011). Thus, certain tree cover values in relation to the territory size of a species as well as gradients in tree density as suitable habitats are crucial for maintaining or restoring substantial population sizes of different species. However, niche space is multidimensional (GREGORY & VAN STRIEN 2010), and we further found these species being associated to certain habitat types or groups of habitat types. Among the investigated species, Tree Pipit, Yellowhammer, and Red-backed Shrike, despite negative short-term population trends in the first two species (GERLACH et al. 2019), are ranked common species, while European Nightjar and Woodlark are considered semi-frequent or in the case of Barred Warbler even rare species in Germany (GRÜNEBERG et al. 2015). While the common species were associated with common habitat types (coniferous forest, scrubs and hedges) or did not show any habitat dependency, the semi-frequent birds depended on heathlands, which count towards the threatened habitats according to the EU Habitats Directive, and the rare species relied on a mosaic of several threatened habitat types imbedded in semi-open landscapes. This otherwise suggests that especially semi-frequent and rare birds of the semi-open landscape guild may serve as overall highly valuable biodiversity indicators across various trophic levels.

However, as mentioned in the beginning, frequency or rarity alone should not be the main factor considered in conservation management decisions. Population dynamics of common species may also give important information on the state of habitats and ecosystems as well as management implications (GASTON 2008). As a common species, for instance, Tree Pipit is a ground-nesting, long-distance migratory bird, which shows a strong negative population trend across European countries (PECBMS 2019). Specifically, the groups of long-distance migrants, ground- and low-nesting bird species, and bird species with an invertebrate diet have declined significantly over the last decades for different reasons (GREGORY et al. 2007, VICKERY et al. 2014, MALLORD et al. 2016). All of the six keystone species fall at least in one of these groups. That holds implications for the importance of adapting conservation measures for fostering suitable habitats and ecosystem functioning for these species on former MTAs transformed into conservation areas.

5. Conclusion

Semi-open landscapes, defined as sparsely wooded (> 20–46% wood cover) or densely wooded (> 46–68%) transition zones between open habitats and forests, are rare habitats in modern Central European landscapes that are mostly limited to actively used and decommissioned MTAs, and special conservation areas with conserved or newly established traditional (low-intensity, low-nitrogen, small-scale) management practices. They provide habitats for large numbers of threatened bird species that are dependent on different species-specific key resources in a highly variable multidimensional niche space. Preserving or restoring such semi-open landscapes with their immanently high bird diversity requires large-scale management approaches to maintain heterogeneous, patchy mosaics of different successional stages or structural elements with different percentages of wood cover, and associated (often high nature value) habitat types. For our study areas, we defined specific management measures for the restoration and conservation of semi-open landscapes (Supplement S2). Management options should be adapted to the desired keystone species. Here, we provided optimum wood cover values for six keystone bird species of the semi-open habitat guild. For instance, if defined target values for local populations of European Nightjar and Red-backed Shrike, both species of Annex I of the European Birds Directive, are to be attained in a given area, management should focus, for European Nightjar, on maintaining/restoring a mosaic of patches of sparsely wooded successional forest areas (c. 37% wood cover) and heathland, as well as, for Red-backed Shrike, on more open areas with a sufficient number of shrubs and hedges (c. 20% wood cover). The maintenance of shrubs and hedges are features of high nature value (HNV) farmland and are, to a certain extent, eligible under the EU Common Agricultural Policy (CAP). Yet large-scale management of semi-open landscapes with partly higher wood cover values needs dynamic approaches of mechanically resetting forest succession to open pioneer stages, fire management, and/or wood pasture that are cost-intensive and usually economically infeasible. Furthermore, situated at the interface of open land management and forestry responsibility, this inherits substantial conflicts with regard to forest clearing and afforestation policy, and in the current restriction of agricultural eligibility criteria to legally recognised open land. Promoting combined open land-woodland management of semi-open landscapes should thus become a policy priority for adapting EU CAP to the needs of bird conservation.

Erweiterte deutsche Zusammenfassung

Einleitung – Militärische Übungsplätze weisen aufgrund geringer Stickstoffeinträge und einer heterogenen Störungsdynamik, bei der durch verschiedene militärische Aktivitäten fein skalierte Landschaftsmosaike erzeugt werden, eine hohe Anzahl seltener und gefährdeter Pflanzen- und Tierarten und unterschiedlicher Lebensräume auf (GAZENBEEK 2005, WARREN et al. 2007, REIF et al. 2011). Sie ähneln traditionell bewirtschafteten Kulturlandschaften, in denen sich in halboffenen Landschaften auf kleinem Raum verschiedene offene Vegetationstypen und von Gehölzen geprägte Vegetationsformen abwechseln (STOATE et al. 2009, BUŠEK & REIF 2017). Seit den 1990er Jahren wurden in Europa große Teile (rund 1,5 Mio. ha) der militärischen Übungsplätze stillgelegt (ELLWANGER & REITER 2019). In Deutschland wurden davon die meisten in das Nationale Naturerbe übertragen. Die Flächenempfänger stehen nun vor der Herausforderung, umfassende Managementstrategien für die Erhaltung der naturschutzfachlich wertvollen Lebensräume und Arten zu entwickeln. In dieser Studie verwendeten wir die Gilde der Vogelarten, die an halboffene Landschaften gebunden sind, als Indikatorartengruppe. Am Beispiel von 14 ehemaligen militärischen Übungsplätzen (ca. 200 km²) im Norddeutschen Tiefland und im Schichtstufenland Süddeutschlands analysierten wir halboffene Landschaften mit den Zielen, (1) das räumliche Vegetationsmosaik in Hinsicht auf Struktur und Zusammensetzung zu charakterisieren und den Anteil halboffener Landschaften an der Gesamtlandschaft zu quantifizieren, (2) für verschiedene Vogelarten halboffener Landschaften die benötigten Lebensraumressourcen zu ermitteln und die Gefährdungssituation der Vogelarten in Abhängigkeit von der Ressourcenverfügbarkeit einzuordnen, und (3) Managementempfehlungen für typische Vogelarten der halboffenen Landschaften zu geben.

Methoden – In allen Untersuchungsgebieten wurde eine flächendeckende Biotoptypenkartierung nach standardisierter Methodik durchgeführt. Für jedes Biotop wurden zwei Merkmalsklassen abgeleitet: (a) die prozentuale Gehölzbedeckung (unter Berücksichtigung zusätzlicher Daten aus der Forsteinrichtung), (b) die Vegetationsformation (Bundescode nach FINCK et al. 2017). Seltene, mittelhäufige und geschützte häufige heimische Brutvogelarten wurden mittels Revierkartierung nach dem methodischen Standard von SÜDBECK et al. (2005) erfasst. Die Landschaftsanalyse erfolgte zum einen auf der Skala des gesamten Untersuchungsgebiets in 1-ha-Rasterfeldern (Landschaftsebene), zum anderen in den Landschaftsausschnitten der Brutvogelreviere (Revierebene). Auf Landschaftsebene wurden fünf Gehölzbedeckungsklassen mit Hilfe des *k*-Mittelwert-Algorithmus (MACKAY 2005) ermittelt und ihre räumliche Anordnung mit dem Anselin Local Moran's I (ANSELIN 1995) untersucht. Auf Revierebene wurde für eine Auswahl von sechs typischen Brutvogelarten halboffener Landschaften Unterschiede in der Gehölzbedeckung unter Verwendung von linearen gemischten Modellen (LME) und differenzierende Vegetationsformationen anhand des Differentialarten-Algorithmus nach TSIRIPIDIS et al. (2009) ermittelt.

Ergebnisse – Wir definierten halboffene Landschaften als spärlich bewaldete (> 20−46 % Gehölzbedeckung) bis dicht bewaldete (> 46−68 %) Übergangszonen zwischen Offenland und Wald. Halboffene, gehölzdominierte (≥ 68%) und geschlossen bewaldete (≥ 87 %) Landschaften bildeten großräumig zusammenhängende Ökotone, während offene Landschaften (≤ 20 %) räumlich geklumpt auf nur 12 % der Gesamtfläche auftraten. Von insgesamt 6476 Brutrevieren war die an halboffene Landschaften gebundene Vogelgilde außergewöhnlich groß und machte 61 % der Individuenzahl und 71 % aller gefährdeten Vögel aus, während die gesamte halboffene Fläche nur 28 % betrug. Die sechs ausgewählten typischen Brutvogelarten halboffener Landschaften (Baumpieper, Ziegenmelker, Goldammer, Neuntöter, Heidelerche und Sperbergrasmücke) waren von verschiedenen artenspezifischen Schlüsselressourcen abhängig (optimale prozentuale Gehölzbedeckung, einzelne oder eine Kombination von Vegetationsformationen). Beispielsweise besetzte der Ziegenmelker ein Mosaik aus Sukzessionswäldern (ca. 37 % Gehölzbedeckung) und Heiden, während der Neuntöter offenere Flächen mit einer ausreichenden Menge an Gebüschen und Hecken (ca. 20 % Gehölzbedeckung) benötigte. Generell galt, dass eine Vogelart umso spezifischere Ressourcen benötigte, je seltener sie war.

Fazit – Halboffene Landschaften als Mosaike verschiedener Sukzessionsstadien oder Strukturelemente mit unterschiedlicher Gehölzbedeckung können nur durch großräumig angelegte Managementansätze dauerhaft erhalten oder wiederhergestellt werden. Auf Grundlage der hier ermittelten artspezifischen optimalen Gehölzbedeckungswerte in Kombination mit den benötigten Vegetationsformationen können in Europäischen Vogelschutzgebieten konkrete Managementvorgaben gemacht werden (vgl. Beilage S2), um bestimmte Zielwerte für lokale Populationen von beispielsweise Ziegenmelker und Neuntöter zu erreichen. Da halboffene Landschaften an der Schnittstelle zwischen landwirtschaftlichem und forstwirtschaftlichem Verantwortungsbereich liegen, kommt es bei der Erhaltung dieser Landschaften mithilfe von dynamischen Ansätzen häufig zu Konflikten in Bezug auf Waldrodungsverbote und Aufforstungspolitik auf der einen Seite und in Bezug auf Kriterien für die Förderfähigkeit von landwirtschaftlich genutzten Flächen auf der anderen Seite. Dies sollte bei der Anpassung der neuen Gemeinsamen Agrarpolitik (GAP) Berücksichtigung finden.

Liste der sechs ausgewählten typischen Brutvogelarten halboffener Landschaften:
Baumpieper – Tree Pipit (*Anthus trivialis*)
Ziegenmelker – European Nightjar (*Caprimulgus europaeus*)
Goldammer – Yellowhammer (*Emberiza citrinella*)
Neuntöter – Red-backed Shrike (*Lanius collurio*)
Heidelerche – Woodlark (*Lullula arborea*)
Sperbergrasmücke – Barred Warbler (*Sylvia nisoria*)

Acknowledgements

We thank the staff of the consultant offices BioM (Jarmshagen), BIOS (Osterholz-Scharmbeck), Büro für ökologische Studien Schlumprecht (Bayreuth), GFN Umweltpartner (Hinzdorf), institut biota (Bützow), IVL (Hemhofen), LPR Reichhoff (Dessau-Roßlau), LUP (Potsdam), naturplan (Darmstadt), ÖFA (Schwabach), RANA Frank Meyer (Halle/Saale), Siedlung und Landschaft Ludloff (Luckau), Triops (Halle/Saale), and UmweltPlan (Stralsund) for their qualified and thorough work on bird and habitat surveys. Dominik Poniatowski and Charlotte Seifert participated in the quality control of habitat mapping projects. Ioannis Tsiripidis and Erwin Bergmeier shared their Excel tool and user manual for calculating fidelity measures.

Author contributions

H.C. conceived the idea and wrote the paper. B.E., H.C. and T.L. prepared the data. H.C., B.E. and K.W. performed statistical analysis. All authors commented on the text and discussed the results.

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Supplements

Supplement S1. Abundances of bird species of semi-open landscapes with probable or confirmed breeding (territories of EOAC categories ‘B’ or ‘C’) in 14 national natural heritage areas in Germany.

Beilage S1. Häufigkeit der Vogelarten halboffener Landschaften mit wahrscheinlicher oder bestätigter Brut (Reviere der EOAC-Kategorien „B“ oder „C“) auf 14 Naturerbeflächen.

Supplement S2. Examples of management measures for the restoration and conservation of semi-open landscapes that have been implemented or are planned to be implemented in the forthcoming 10 years in the study areas according to natural heritage management plans.

Beilage S2. Beispiele für Bewirtschaftungsmaßnahmen zur Wiederherstellung und Erhaltung von halboffenen Landschaften nach Naturerbe-Entwicklungsplänen, die bereits umgesetzt wurden oder in den kommenden 10 Jahren in den Untersuchungsgebieten durchgeführt werden sollen.

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Structural configuration of landscapes.

Anhang E1. Strukturelle Konfiguration von Landschaften.

Supplement E2. Results of descriptive and linear mixed-effects model (LME) statistics of occurrences of six breeding bird species of semi-open landscapes in dependency of the wood cover (in %) in their territories.

Anhang E2. Ergebnisse der deskriptiven und linearen Mixed-Effects-Modell (LME)-Statistik des Vorkommens von sechs Brutvogelarten halboffener Landschaften in Abhängigkeit von der Gehölzbedeckung (in %) in ihren Territorien.

References

ANSELIN, L. (1995): Local indicators of spatial association – LISA. – Geogr. Anal. 27: 93–115.

AYCRIGG, J.L., BELOTE, R.T., DIETZ, M.S., APLET, G.H. & FISCHER, R.A. (2015): Bombing for biodiversity in the United States: Response to Zentelis & Lindenmayer 2015. – Conserv. Lett. 8: 306–307.

BAKX, T.R.M., LINDSTRÖM, A., RAM, D., PETTERSSON, L.B., SMITH, H.G., VAN LOON, E.E. & CAPLAT, P. (2020): Farmland birds occupying forest clear-cuts respond to both local and landscape features. – Forest Ecol. Manag. 478: 118519.

BÁLDI, A. & BATÁRY, P. (2011): Spatial heterogeneity and farmland birds: different perspectives in Western and Eastern Europe. – Ibis 153: 875–876.

BATES, D., MÄCHLER, M., BOLKER, B. & WALKER, S. (2015): Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

BATES, D., MÄCHLER, M., BOLKER, B. … FOX, J. (2019): Linear Mixed-Effects Models using 'Eigen' and S4. Package 'lme4', v. 1.1-21. – URL: https://cran.r-project.org/web/packages/lme4/lme4.pdf [accessed January 2020].

BAUER, H.G., BEZZEL, E. & FIEDLER, W. (2005): Das Kompendium der Brutvögel Mitteleuropas. 2. Vol., 2nd ed. – Aula-Verlag, Wiesbaden: 1767 pp.

BENTON, T.G., VICKERY, J.A. & WILSON, J.D. (2003): Farmland biodiversity: is habitat heterogeneity the key? – Trends Ecol. Evol. 18: 182–188.

BMU (2017): Das Nationale Naturerbe. Naturschätze für Deutschland. Federal Ministry for the Environment, Nature Conservation and Nuclear Safety. – URL: https://www.bmu.de/fileadmin/Daten_BMU/Pools/Broschueren/nat_naturerbe_bf.pdf [accessed January 2020].

BNATSCHG (2009): Bundesnaturschutzgesetz (Gesetz über Naturschutz und Landschaftspflege), 29/07/2009, BGB1. I p. 2542 (last changed Art. 8, 13/05/2019, BGB1. I p. 706).

BUŠEK, O. & REIF, J. (2017): The potential of military training areas for bird conservation in a central European landscape. – Acta Oecol. 84: 34–40.

CHYTRÝ, M., TICHÝ, L., HOLT, J. & BOTTA-DUKÁT, Z. (2002): Determination of diagnostic species with statistical fidelity measures. – J. Veg. Sci. 13: 79–90.

ČÍŽEK, O., VRBA, P., BENEŠ, J., HRÁZSKÝ, Z., KOPTÍK, J., KUČERA, T., MARHOUL, P., ZÁMEČNÍK, J. & KONVIČKA, M. (2013): Conservation potential of abandoned military areas matches that of established reserves: plants and butterflies in the Czech Republic. – PLOS one 8: e53124.

DAVIES, C.E., MOSS, D. & HILL, M.O. (2004): EUNIS habitat classification revised 2004. – European Environment Agency, Copenhagen.

DOER, D., MELTER, J. & SUDFELDT, C. (2002): Ornithological criteria for selection of Important Bird Areas in Germany. – Ber. Vogelschutz 38: 111–155.

DUNNING, J.B., DANIELSON, B.J. & PULLIAM, H.R. (1992): Ecological processes that affect populations in complex landscapes. – Oikos 65: 169–175.

DWD (DEUTSCHER WETTERDIENST) (2019): Grids of the multi-annual means over Germany 1981–2010. – URL: https://opendata.dwd.de/climate_environment/CDC/grids_germany/multi_annual/ [accessed July 2019].

EGGERS, B., MATERN, A., DREES, C., EGGERS, J., HÄRDTLE, W. & ASSMANN, T. (2010): Value of Semi-Open Corridors for Simultaneously Connecting Open and Wooded Habitats: a Case Study with Ground Beetles. – Conserv. Biol. 24: 256–266.

ELLWANGER, G. & REITER, K. (2019): Nature conservation on decommissioned military training areas – German approaches and experiences. – J. Nat. Conserv. 49: 1–8.

EURING (2019): Species code based on the EURING exchange code 2000+. Last updated 04/10/19. – URL: https://app.bto.org/euringcodes/species.jsp [accessed: 2019-12-10].

FINCK, P., HEINZE, S., RATHS, U., RIECKEN, U. & SSYMANK, A. (2017): Rote Liste der gefährdeten Biotoptypen Deutschlands. 3rd ed. – Naturschutz Biol. Vielfalt 156: 1–637.

FLADE, M. (1994): Brutvogelgemeinschaften Mittel- und Norddeutschlands. Grundlagen für den Gebrauch vogelkundlicher Daten in der Landschaftsplanung. – IHW-Verlag, Eching: 879 pp.

FRANKENBERG, P. (1991): Moderne Klimakunde. – Westermann-Verlag, Braunschweig: 128 pp.

GASTON, K.J. (2008): Biodiversity and extinction: the importance of being common. – Prog. Phys. Geogr. 32: 73–79.

GASTON, K.J., JACKSON, S.F., NAGY, A., CANTE-SALAZAR, L. & JOHNSON, M. (2008): Protected areas in Europe. Principle and practice. – Ann. NY Acad. Sci. 1134: 97–119.

GAUER, J. & ALDINGER, E. (Eds.) (2005): Waldökologische Naturräume Deutschlands. Forstliche Wuchsgebiete und Wuchsbezirke, mit Karte 1:1 000 000. – Mitt. Ver. Forstl. Standortskd. Forstpflanzenzüchtung 43: 1–324.

GAZENBEEK, A. (2005): LIFE, Natura 2000 and the military. Life Focus – Journal of the European Commission, Environment Directorate General Life III Program (2000–2006).

GERLACH, B., DRÖSCHMEISTER, R., LANGGEMACH, T. … SUDFELDT, C. (2019): Vögel in Deutschland – Übersichten zur Bestandssituation. – DDA, BfN, LAG VSW, Münster: 64 pp.

GILL, F. & DONSKER, D. (Eds.) (2019): IOC World Bird List (v 9.2). – Doi: 10.14344/IOC.ML.9.2. – URL: http://www.worldbirdnames.org/ [accessed: 2019-12-10].

GLUTZ VON BLOTZHEIM, U. & BAUER, K.M. (Eds.) (1998): Handbuch der Vögel Mitteleuropas. 14 Vol. – Aula-Verlag, Wiesbaden.

GREGORY, R.D. & GASTON, K.J. (2000): Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. – Oikos 88: 515–526.

GREGORY, R.D., SKORPILOVA, J., VOŘÍŠEK, P. & BUTLER, S. (2019): An analysis of trends, uncertainty and species selection shows contrasting trends of widespread forest and farmland birds in Europe. – Ecol. Indic. 103: 676–687.

GREGORY, R.D. & VAN STRIEN, A. (2010): Wild bird indicators: using composite population trends of birds as measures of environmental health. – Ornithol. Sci. 9: 3–22.

GREGORY, R.D., VOŘÍŠEK, P., VAN STRIEN, A., GMELIG MEYLING, A.W., JIGUET, F., FORNASARI, L., REIF, J., PRZEMYSŁAW, P. & BURFIELD, I. (2007): Population trends of widespread woodland birds in Europe. – Ibis 149 (Suppl. 2): 78–97.

GRÜNEBERG, C., BAUER, H.G., HAUPT, H., HÜPPOP, O., RYSLAVY, T. & SÜDBECK, P. (2015): Rote Liste der Brutvögel Deutschlands. 5. Fass., 30/11/2015. – Ber. Vogelschutz 52: 19–67.

HAGEMEIJER, W.J.M. & BLAIR, M.J. (1997): The EBCC atlas of European breeding birds: their distribution and abundance. – European Bird Census Council, London: 903 pp.

HANSPACH, J., FISCHER, J., STOTT, J. & STAGOLI, K. (2011): Conservation management of eastern Australian farmland birds in relation to landscape gradients. – J. Appl. Ecol. 48: 523–531.

HILMERS, T., FRIESS, N., BÄSSLER, C., HEURICH, M., BRANDL, R., PRETZSCH, H., SEIDL, R. & MÜLLER, J. (2018): Biodiversity along temperate forest succession. – J. Appl. Ecol. 55: 2756–2766.

INGER, R., GREGORY, R., DUFFY, J.P., STOTT, I., VOŘÍŠEK, P. & GASTON, K.J. (2015): Common European birds are declining rapidly while less abundant species' numbers are rising. – Ecol. Lett. 18: 28–36.

JENTSCH, A., FRIEDRICH, S., STEINLEIN, T., BEYSCHLAG, W. & NEZADAL, W. (2009): Assessing conservation action for substitution of missing dynamics on former military training areas in central Europe. – Restor. Ecol. 17: 107–116.

JULLIARD, R., CLAVEL, J., DEVICTOR, V., JIGUET, F. & COUVET, D. (2006): Spatial segregation of specialists and generalists in bird communities. – Ecol. Lett. 9: 1237–1244.

KUZNETSOVA, A., BROCKHOFF, P.B., CHRISTENSEN, R.H.B. & JENSEN, S.P. (2019): Tests in Linear Mixed Effects Models. Package 'lmerTest', v. 3.1-1. – URL: https://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf [accessed January 2020].

LORENZ, A., SEIFERT, R., OSTERLOH, S. & TISCHEW, S. (2016): Which conservation goals can we achieve by low-intensity grazing management with large herbivores? – Natur und Landschaft 91: 73–82.

MACKAY, D. (2005): Information Theory, Inference and Learning Algorithms. V. 7.2, 4th printing. – Cambridge University Press, Cambridge: 628 pp.

MALLORD, J.W., SMITH, K.W., BELLAMY, P.E., CHARMAN, E.C. & GREGORY, R.D. (2016): Are changes in breeding habitat responsible for recent population changes of long-distance migrant birds? – Bird Study 63:1–12.

MCGARIGAL, K. (2015): FRAGSTATS help. Documentation, 21/04/2015. – URL: https://www.umass.edu/landeco/research/fragstats/documents/fragstats.help.4.2.pdf [accessed: 2019-12-30].

PAQUET, J.Y., VANDERVYVRE, X., DELAHAYE, L. & RONDEUX, J. (2006): Bird assemblages in a mixed woodland-farmland landscape: The conservation value of silviculture-dependant open areas in plantation forest. – For. Ecol. Manag. 227: 59–70.

PECBMS (Pan-European Common Bird Monitoring Scheme) (2019): European wild bird indicators, 2019 update. – URL: https://pecbms.info/european-wild-bird-indicators-2019-update/ [accessed: 2020-04-16].

PERINGER, A., SIEHOFF, S., CHÉTELAT, J., SPIEGELBERGER, T., BUTTLER, A. & GILLET, F. (2013): Past and future landscape dynamics in pasture-woodlands of the Swiss Jura Mountains under climate change. – Ecol. Soc. 18 (3): 11.

R CORE TEAM (2019): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. – URL: https://www.R-project.org/.

REIF, J., MARHOUL, P., ČÍŽEIK, O. & KONVIČKA, M. (2011): Abandoned military training sites are an overlooked refuge for at-risk open habitat bird species. – Biodiv. Conserv. 20: 3645–3662.

REIF, J., MARHOUL, P. & KOPTÍK, J. (2013): Bird communities in habitats along a successional gradient: Divergent patterns of species richness, specialization and threat. – Basic Appl. Ecol. 14: 423–431.

REITER, K. & DOERPINGHAUS, A. (2015): Germany’s National Natural Heritage scheme – defining assets, taking stock, looking ahead. – Natur und Landschaft 90: 98–104.

RÖSCH, V., HOFFMANN, M., DIEHL, U. & ENTLING, M.H. (2019): The value of newly created wood pastures for bird and grasshopper conservation. – Biol. Conserv. 237: 493–503.

RSTUDIO TEAM (2019): RStudio: Integrated Development for R. – RStudio, Inc., Boston, MA. – URL: http://www.rstudio.com/.

SCHULZE, M., MEYER, F. & FISCHER, S. (2015): Importance of the Special Protection Areas of Saxonia-Anhalt dominated by *Calluna* heathland for the conservation of indicator species of sandy heaths and their management. – Ber. Vogelschutz 52: 79–97.

STOATE, C., BÁLDI, A., BEJA, P., BOATMAN, N.D., HERZON, I., VAN DOORN, A., DE SNOO, G.R., RAKOSY, L. & RAMWELL, C. (2009): Ecological impacts of early 21st century agricultural change in Europe – A review. – J. Environ. Manag. 91: 22–46.

SÜDBECK, P., ANDRETZKE, H., FISCHER, S., GEDEON, K., SCHIKORE, T., SCHRÖDER, K. & SUDFELDT, C. (Eds.) (2005): Methodenstandards zur Erfassung der Brutvögel Deutschlands. – Radolfzell.

SÜDBECK, P., BAUER, H.G., BOSCHERT, M., BOYE, P. & KNIEF, W. (2007): Rote Liste der Brutvögel Deutschlands. 4th ed., 30/11/2007. – Ber. Vogelschutz 44: 23–81.

SUTCLIFFE, L.M.E., BATÁRY, P., KORMANN, U. … TSCHARNTKE, T. (2015): Harnessing the biodiversity value of Central and Eastern European farmland. – Divers. Distrib. 21: 722–730.

TSIRIPIDIS, I., BERGMEIER, E., FOTIADIS, G. & DIMOPOULOS, P. (2009): A new algorithm for the determination of differential taxa. – J. Veg. Sci. 20: 233–240.

VICKERY, J.A., EWING, S.R., SMITH, K.W., PAIN, D.J., BAIRLEIN, F., ŠKORPILOVÁ, J. & GREGORY, R.D. (2014): The decline of Afro-Palaearctic migrants and an assessment of potential causes. – Ibis 156: 1–22.

VIVAND, R., ONO, H., DUNLAP, R., STIGLER, M. & VENNEY, B. (2019): Choose Univariate Class Intervals. Package ‘classInt’, v. 0.4-2. – URL: https://github.com/r-spatial/classInt/ [accessed January 2020].

WARREN, S.D., HOLBROOK, S.W., DALE, D.A., WHELAN, N.L., ELYN, M., GRIMM, W. & JENTSCH, A. (2007): Biodiversity and the heterogeneous disturbance regime on military training lands. – Restor. Ecol. 15: 606–612.

WIENS, J.A. (1976): Population responses to patchy environments. – Annu. Rev. Ecol. Syst. 7: 81–120.

Supplement S1. Abundances of bird species of semi-open landscapes with probable or confirmed breeding (territories of EOAC categories 'B' or 'C') in 14 national natural heritage areas in Germany. Red list category (RL, cp. Fig. 3, asterisks indicate species included in Annex I of the Birds Directive) and estimated population sizes in Germany (Pop. size: R, rare; S, semi-frequent; F, frequent) derived from GRÜNEBERG et al. (2015). Species-specific mean home ranges during the breeding season (territory, in ha) were compiled from literature. Because of their special breeding ecology, no home range was assigned (n/a) for host-breeding Common Cuckoo (*Cuculus canorus*), and colony-breeding Common Starling (*Sturnus vulgaris*) and Hooded Crow (*Corvus cornix*). In addition, the area of estimated suitable habitats of semi-open landscapes (sum of wood cover class c2 and c3, in ha) is given with derived values of estimated bird density (*n*/ha). Species in bold letters were selected for further habitat-related analysis. Compare Table 1 for study area acronyms.

Beilage S1. Häufigkeit der Vogelarten halboffener Landschaften mit wahrscheinlicher oder bestätigter Brut (Reviere der EOAC-Kategorien „B“ oder „C“) auf 14 Naturerbeflächen. Rote-Liste-Kategorie (RL, vgl. Abb. 3; Sternchen kennzeichnen Arten des Anhangs I der Europäischen Vogelschutzrichtlinie) und geschätzte Populationsgrößen in Deutschland (R, selten; S, mittelhäufig; F, häufig) nach GRÜNEBERG et al. (2015). Artspezifische mittlere Brutreviergrößen (Territorium, in ha) wurden der Literatur entnommen. Aufgrund der speziellen Brutökologie von Kuckuck (*Cuculus canorus*), Star (*Sturnus vulgaris*) und Nebelkrähe (*Corvus cornix*) wurden für diese Arten keine Reviergrößen angegeben (n/a). Zusätzlich wurde die Fläche der geschätzten geeigneten Lebensräume halboffener Landschaften (Summe der Gehölzbedeckungsklassen c2 und c3, in ha) mit abgeleiteten Werten der geschätzten Vogeldichte (*n* ha-1) angegeben. Fettgedruckte Arten wurden für die weitere Analyse des Lebensraums ausgewählt. Vgl. Tabelle 1 für Akronyme der Untersuchungsgebiete.

Species (scientific)	Species (English)	Family	RL	Pop. size	Territory (ha)	CU	PR	PE	UE	RH	RO	KH	OH	GH	WE	ME	RW	TE	HB	Sum
Anthus trivialis	Tree Pipit	Motacillidae	3	F	1.0	72	117	103	219	366	7	23	179	286	36	77	54	47		1,586
Caprimulgus europaeus	European Nightjar	Caprimulgidae	3*	R	1.5	6			1	6		4	53	82	6			15		173
Carpodacus erythrinus	Common Rosefinch	Fringillidae	LC	R	1.0			4	3											7
Corvus cornix	Hooded Crow	Corvidae	LC	S	n/a		5	1												6
Cuculus canorus	Common Cuckoo	Cuculidae	NT	S	n/a	3		17	15	1	2	9	4	7	1	14	5	7		85
Emberiza citrinella	Yellowhammer	Emberizidae	NT	F	0.5	40		44	86	12	3	32	59	14	14	111	79	43	30	567
Jynx torquilla	Eurasian Wryneck	Picidae	2	S	10		4		3		1	1	17		1	12	9	6	3	57
Lanius collurio	Red-backed Shrike	Laniidae	LC*	F	1.5	36	93	57	39	3	2	20	24	11	5	16	9	11	12	338
Lanius excubitor	Great Grey Shrike	Laniidae	2	R	40				1			1	3	2	1					8
Linaria cannabina	Common Linnet	Fringillidae	3	F	0.1	3	4	12	1	1			10	1	2	2	2			38
Locustella fluviatilis	River Warbler	Locustellidae	LC	R	0.4		7	6	9		2									24
Locustella naevia	Common Grasshopper Warbler	Locustellidae	3	S	0.3		2	15	7		2	4						1		31
Lullula arborea	Woodlark	Alaudidae	NT*	S	2.5	35	3		40	25		44	132	56	31	18	12	26	5	427
Luscinia luscinia	Thrush Nightingale	Muscicapidae	LC	S	1.0		16	26												42
Phoenicurus phoenicurus	Common Redstart	Muscicapidae	NT	S	1.0	8		26	38	69		12	1	8	2	16	32	10	2	224
Picus viridis	European Green Woodpecker	Picidae	LC	S	200			3	13	4	5	8	4	2	3	8	6	2	7	65
Streptopelia turtur	European Turtle Dove	Columbidae	2	S	7.5									1		4				5
Sturnus vulgaris	Common Starling	Sturnidae	3	F	n/a			9	55		26	26	12		5	15	6	4	35	193
Sylvia nisoria	Barred Warbler	Sylviidae	3*	R	1.5		10	18				2	4							34
Upupa epops	Eurasian Hoopoe	Upupidae	3	R	70				1				21	1	3				1	27
Sum of bird counts (*n*)						**203**	**261**	**341**	**531**	**487**	**50**	**186**	**523**	**471**	**110**	**293**	**214**	**172**	**95**	**3,937**
Habitat area (c2+c3) (ha)						262	829	287	619	492	113	376	695	1,251	119	124	131	175	77	5,548
Bird density (*n*/ha)						0.8	0.3	1.2	0.9	1.0	0.4	0.5	0.8	0.4	0.9	2.4	1.6	1.0	1.2	0.7

Supplement S2. Examples of management measures for the restoration and conservation of semi-open landscapes that have been implemented or are planned to be implemented in the forthcoming 10 years in the study areas according to natural heritage management plans.

Beilage S2. Beispiele für Bewirtschaftungsmaßnahmen zur Wiederherstellung und Erhaltung von halboffenen Landschaften nach Naturerbe-Entwicklungsplänen, die bereits umgesetzt wurden oder in den kommenden 10 Jahren in den Untersuchungsgebieten durchgeführt werden sollen.

	Study area	Measure unit	Management area (ha)	Associated plant communities	Target bird species	Management measures
1	Cuxhavener Küstenheiden (CU)	1a	280	*Calluna* heathland, *Nardion* grassland, and other nutrient-poor grasslands	Red-backed Shrike, Woodlark	Extensive rotational paddock grazing by horses and cattle, maintaining 10% of wood cover (shrubs, trees) in open land
		1b	178	*Empetrum* heathlands	Red-backed Shrike, Woodlark, Great Grey Shrike	Extensive grazing by sheep and goats, maintaining 10% of scrubs and solitary trees
		1c	17	Ruderal forbs and grasslands at forest fringes and edges	Tree Pipit, European Nightjar	Irregular removal of shrubs and successional trees
		1d	14	Pine forest	European Nightjar	Thinning of pine forest to 40% wood cover
		1e	44	Pine forest	Red-backed Shrike, Tree Pipit, Common Redstart	Creation of structured forest-open land transition zones (c. 30m width) by irregular removal of trees
		1f	30	Oak, larch, and pine field woods	Tree Pipit, European Nightjar	Woodland pasture by horses and cattle
2	Prora (PR)	2a	40	*Calluna* heathland, nutrient-poor grasslands	Red-backed Shrike, Barred Warbler, Woodlark	Extensive grazing by cattle and water buffalos, maintaining 10% of scrubs and solitary trees
		2b	17	*Juniperus communis* formation on heath over flint-stone beach wall formation	Red-backed Shrike, Barred Warbler	Removal of young trees, scrubs, and topsoil, structuring of neighbouring forest fringes, and, optionally, grazing by sheep and goats
		2c	17	Wet grasslands	Red-backed Shrike	Extensive grazing by cattle, maintaining single scrubs
		2d	36	*Molinion* grassland, *Erica tetralix* heathland, *Caricion davallianae* and *Cladion mariscus* fens	Red-backed Shrike	Extensive mowing, removal of successional trees, but maintaining solitary shrubs and neighbouring small forest patches in the wetland complex
		2e	12	Successional forest	Tree Pipit	Woodland pasture by cattle, partly accompanied by manual thinning
		2f	17	Plantations of native deciduous trees and forest fringes	Red-backed Shrike, Tree Pipit, Barred Warbler	Creation of structured forest-open land transition zones by irregular removal of trees
		2g	28	Sand and ruderal grassland, *Sarothamnus scoparius* scrubs	Red-backed Shrike, Barred Warbler	Extensive grazing by sheep, removal of broom and successional trees
		2h	107	Complex of fresh and wet grasslands, and forb communities	Red-backed Shrike, Barred Warbler, Eurasian Wryneck	Extensive grazing by sheep and goats, removal of successional trees
3	Peenemünde (PE)	3a	170	Marshes and salt meadows (*Glauco-Puccinellietalia maritimae*, *Thero-Salicornietea*) with scattered juniper and dog rose scrubs (150 ha); birch-oak mixed forest (20 ha)	Red-backed Shrike, Barred Warbler	Rotational paddocks and wood pasture with extensive cattle grazing
		3b	9	Successional forest and field scrubs (in complex with ruderal grasslands)	Red-backed Shrike	Wood pasture
		3c	13	Forest fringes	Tree Pipit	Creation of structured forest-open land transition zones by irregular removal of trees
4	Ueckermünder Heide (UE)	4a	178	Pine, oak, and birch mixed forests on sandy soils (159 ha), in complex with grasslands and *Calluna* heathland (19 ha)	Tree Pipit, Red-backed Shrike	Thinning of forests to < 70% wood cover, rotational set back of successional stages, wood pasture
5	Rüthnicker Heide (RH)	5a	80	Pine forest and successional forest fringing *Calluna* heathland	Tree Pipit, Woodlark, European Nightjar	Thinning of forests to 40% wood cover, irregularly looping up to 30-50m deep from open land to forest
		5b	170	*Calluna* heathland, nutrient-poor grassland, open sand, and successional forest	Tree Pipit, Woodlark, European Nightjar	Removal of successional shrubs and trees, and heath by mowing every 6-8 years
6	Roßlauer Elbauen (RO)	6a	7	Floodplain woodlands	Red-backed Shrike	Wood pasture (goats, sheep, and donkeys) for creating semi-open forests and gradual forest fringes
7	Kühnauer Heide (KH)	7a	170	Xeric sand calcareous grassland, (*Koelerion glaucae*), inland dunes with *Corynephorus* and *Agrostis*, *Calluna* heathland, and *Calamagrostis* grassland (130ha), in complex with oak woods and successional forests	Woodlark, Red-backed Shrike, Barred Warbler, Great Grey Shrike	Extensive sheep and goat grazing (incl. wood pasture) in combination with regular removal of successional shrubs and trees
8	Oranienbaumer Heide (OH)	8a	800	*Calluna* heathland, xeric sand calcareous grassland (*Koelerion glaucae*), inland dunes with open *Corynephorus* and *Agrostis* grassland, dry sand heath with *Calluna* and *Genista*, other sand grasslands, and 236 ha semi-open successional forest	Red-backed Shrike, Barred Warbler, Woodlark, Great Grey Shrike, Eurasian Hoopoe, European Nightjar	Extensive all-year grazing by cattle and horses; in successional forest, in addition to wood pasture, 37 ha are cleared by retaining prominent solitary trees and small groups of trees, 49 ha are thinned to 40% wood cover, and 21 ha are structurally thinned to 70% wood cover
		8b	140	Successional forest, with some patches of *Calluna* heathland, *Calamagrostis* grasslands, and other grassland types	European Nightjar	Creation of structured forest-open land transition zones by irregular removal of trees, partially thinning to 40% wood cover (17 ha)
9	Glücksburger Heide (GH)	9a	990	*Calluna* heathland (686 ha), *Nardion* grassland, sandy nutrient-poor *Corynephorus* grassland, *Calamagrostis* grassland, and birch-pine or pine successional forests	European Nightjar, Woodlark, Tree Pipit, Red-backed Shrike, Great Grey Shrike, Eurasian Hoopoe	Conservation of *Calluna* heathland by grazing (goats and sheep), manual removal of successional trees (retaining max. 10% of solitary or groups of trees), heath mowing, and controlled burning (355 ha); restoration of *Calluna* heathlands by rotational complete removal of successional forests, partly accompanied by grazing or heath biomass removal (405 ha); thinning of successional forests to 40% wood cover, partly accompanied by grazing (230 ha)
		9b	5	Forest fringes (in transition to wet meadows)	Tree Pipit, Woodlark	Creation of structured forest-open land transition zones by irregular removal of trees
10	Weißhaus (WE)	10a	43	*Calluna* heathland, dry grassland, Calamagrostis grassland, and successional forest	Red-backed Shrike, Woodlark, Great Grey Shrike, Eurasian Hoopoe	Extensive grazing with sheep and goats, removal of successional trees (<10%) (34 ha); creation of structured forest-open land transition zones (c. 30m width) by irregular removal of trees (9 ha)
		10b	105	Pine forest with *Vaccinium myrtillus* undergrowth (*Vaccinio-Pinetum*)	Tree Pipit, Woodlark	Creation of structurally rich, sparse forests with manifold inner forest fringes (originally conceived as a species conservation measure for re-introduced Wood Grouse, *Tetrao urogallus*)
11	Mellrichstadt (ME)	11a	133	Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*), *Juniperus communis* formations on calcareous grasslands, mesophilic meadows, thermophilic forest fringes and shrublands, and sparse pine forests	Woodlark, Red-backed Shrike	Extensive mowing of grasslands and meadows (one cut per year) by conserving single trees and scrubs; in *Juniperus* formations pasture by goats in combination with mowing of *Prunus spinosa* stands; creation of structured forest-open land transition zones; conservation of sparse (light-flooded) pine forests
12	Reiterswiesen (RW)	12a	19	Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*), pine and oak woods	Red-backed Shrike, Woodlark, Tree Pipit	Sheep grazing, removal of shrubs if required, creation of structured forest-open land transition zones
		12b	7	Sparse pine forests (in neighbourhood to grasslands)	Tree Pipit	Wood pasture by sheep
		12c	83	*Galio-Carpinetum* oak-hornbeam forest	Tree Pipit	Coppice with standards management (management of c. 40% of the forest area within 10 yrs on 1-3 ha parcels with stocking rate of c. 30-40% wood cover)
13	Tennenlohe (TE)	13a	24	Pine forest fringes (surrounding 63 ha of open land with *Calluna* heathland, inland dunes with open *Corynephorus* and *Agrostis* grassland, dry sand heath with *Calluna* and *Genista*, and *Calamagrostis* grassland)	European Nightjar, Tree Pipit	Creation of structured forest-open land transition zones, partly in combination with wood pasture (Przewalski horses, goats)
14	Hainberg (HB)	14a	103	Park landscape with nutrient-poor grasslands, interspersed scrubs, solitary trees, and field woods	Woodlark, Red-backed Shrike	Grazing by sheep and goats, removal of shrubs if required, and wood management

Supplement E1. Structural configuration of landscapes. Given are the numbers of 1 ha landscape units (*n*), the respective habitat area (in ha) and proportions of landscapes related to the habitat area (in %) in total and by wood cover classes (c1−c5) in 14 national natural heritage areas. Compare Table 1 for study area acronyms and Table 2 for description of landscape types.

Anhang E1. Strukturelle Konfiguration von Landschaften. Angegeben sind die Anzahl der 1 ha großen Landschaftseinheiten (*n*), die jeweilige Lebensraumfläche (in ha) und die Anteile der Landschaften in Bezug auf die Lebensraumfläche (in%) insgesamt und nach Holzbedeckungsklassen (c1-c5) auf 14 Naturerbeflächen. Vergl. Tabelle 1 für die Akronyme der Untersuchungsgebiete und Tabelle 2 für die Beschreibung der Landschaftstypen.

		Number of landscape units (*n*)						Habitat area (ha)							Proportion of landscapes (%)					
		c1	c2	c3	c4	c5	Sum	c1	c2	c3	c4	c5	Sum		c1	c2	c3	c4	c5	Sum
1	CU	359	121	157	445	493	1,575	351	117	145	418	402	1,433		24.5	8.1	10.1	29.2	28.0	100.0
2	PR	347	384	563	522	212	2,028	251	306	523	494	193	1,768		14.2	17.3	29.6	27.9	10.9	100.0
3	PE	734	151	173	226	1,028	2,312	589	129	157	209	942	2,027		29.1	6.4	7.8	10.3	46.5	100.0
4	UE	388	134	593	1,307	948	3,370	200	111	507	1,132	706	2,656		7.5	4.2	19.1	42.6	26.6	100.0
5	RH	50	100	427	1,002	2,547	4,126	49	95	397	939	2,401	3,881		1.3	2.4	10.2	24.2	61.9	100.0
6	RO	138	76	66	56	102	438	98	58	55	43	67	321		30.6	18.2	17.0	13.5	20.8	100.0
7	KH	88	157	252	375	156	1,028	77	149	227	356	149	958		8.1	15.5	23.7	37.2	15.5	100.0
8	OH	385	379	370	619	510	2,263	372	351	344	586	464	2,117		17.6	16.6	16.2	27.7	21.9	100.0
9	GH	246	607	699	797	468	2,817	215	592	659	752	426	2,644		8.1	22.4	24.9	28.5	16.1	100.0
10	WE	43	38	109	516	553	1,259	34	27	92	486	494	1,134		3.0	2.3	8.1	42.9	43.6	100.0
11	ME	68	70	71	29	7	245	53	64	60	27	3	207		25.4	30.9	29.0	13.1	1.6	100.0
12	RW	42	78	81	108	83	392	28	63	68	92	70	321		8.6	19.6	21.2	28.8	21.8	100.0
13	TE	21	85	112	197	91	506	15	79	96	177	71	437		3.4	18.1	22.0	40.4	16.2	100.0
14	HB	109	55	39	35	2	240	95	47	30	24	1	196		48.2	24.1	15.0	12.4	0.3	100.0
	Sum	**3,018**	**2,435**	**3,712**	**6,234**	**7,200**	**22,599**	**2,427**	**2,188**	**3,360**	**5,737**	**6,390**	**20,101**	**Total**	**12.1**	**10.9**	**16.7**	**28.5**	**31.8**	**100.0**
														Mean ± sd	**16.4 ± 13.5**	**14.7 ± 8.2**	**18.1 ± 7.3**	**27.0 ± 11.3**	**23.7 ± 17.1**	**100.0**

Supplement E2. Results of descriptive and linear mixed-effects model (LME) statistics of occurrences of six breeding bird species of semi-open landscapes in dependency of the wood cover (in %) in their territories. GMD is Gini's mean difference. Cover values significantly differ between all species (*p*-values are given for species and species-K_I-interactions). Random effects (*study area*) explained 20% of the variance in the dataset.

Anhang E2. Ergebnisse der deskriptiven und linearen Mixed-Effects-Modell (LME) -Statistik des Vorkommens von sechs Brutvogelarten halboffener Landschaften in Abhängigkeit von der Gehölzbedeckung (in%) in ihren Territorien. GMD: Ginis mittlerer Unterschied. Die Deckungswerte unterscheiden sich signifikant zwischen allen Arten (*p*-Werte sind für Arten und Arten-K_I-Wechselwirkungen angegeben). Zufällige Effekte (Untersuchungsgebiet) erklärten 20% der Varianz im Datensatz.

Species acronym	Species (scientific)	Species (English)	*n*	Mean	GMD	0.25p	0.75p	*p*-of main effect of species	*p*- of species* K_I interaction
AnthTri	***Anthus trivialis***	Tree Pipit	1,586	58.05	33.87	32.84	82.82	3.79e-09 ***	.
CaprEur	***Caprimulgus europaeus***	European Nightjar	173	37.33	24.53	20.26	49.82	0.00035 ***	0.76764
EmbeCit	***Emberiza citrinella***	Yellowhammer	567	28.89	25.68	9.79	43.19	< 2e-16 ***	0.05538 .
LaniCol	***Lanius collurio***	Red-backed Shrike	338	23.79	22.22	8.74	33.95	< 2e-16 ***	0.19402
LullArb	***Lullula arborea***	Woodlark	427	32.02	24.56	15.39	43.26	< 2e-16 ***	0.08836 .
SylvNis	***Sylvia nisoria***	Barred Warbler	34	24.59	18.6	11.17	32.20	0.00302 **	0.03878 *