Bird communities in traditional wood-pastures with changing management in Eastern Europe

Tibor Hartel\textsuperscript{a,b,*}, Jan Hanspach\textsuperscript{b}, David J. Abson\textsuperscript{c}, Orsolya Máthé\textsuperscript{a}, Cosmin Ioan Moga\textsuperscript{d}, Joern Fischer\textsuperscript{b}

\textsuperscript{a} Sapientia Hungarian University of Transylvania, Faculty of Sciences and Arts, Department of Environmental Studies, Cluj-Napoca, Romania
\textsuperscript{b} Faculty of Sustainability, Leuphana University Lüneburg, 21335 Lüneburg, Germany
\textsuperscript{c} FuturES Research Center, Leuphana University Lüneburg, 21335 Lüneburg, Germany
\textsuperscript{d} Ecotransilvania Association, Sighişoara, Romania

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Abstract

Wood-pastures are fragile ecosystems because they were formed by, and depend on specific, low-intensity multifunctional management. Although their ecological and cultural significance is high, wood-pastures are rapidly deteriorating all over Europe, mainly due to changing land use. We still lack a basic understanding of the ecological value of wood-pastures, and in which features they differ from other landscape elements. In this paper we investigated the ecological value of wood-pastures for passerine birds by (i) comparing bird assemblages of wood-pastures with those of closed forests and open pastures and (ii) exploring the relationships between variables describing wood-pastures and species traits of the bird assemblages. Our study region (Southern Transylvania, Romania) provides a unique opportunity to understand the importance of a traditional cultural and ecological environment for many different organisms. Wood-pastures had a higher overall number of bird species, and a higher spatial turnover in bird community composition than closed forests and open pastures. We found significant associations between bird species traits and habitat structural elements in wood-pastures such as large trees, oak- and pear trees and shrubs. Our findings suggest that traditional wood-pastures in Southern Transylvania have distinct and rich passerine bird communities. This richness is inextricably linked to the multifunctional, low-intensity land use traditionally applied in the wood-pastures that promotes high niche diversity. For effective conservation of the biodiversity of wood-pastures, a detailed understanding is needed of how different management regimes may influence the key structural elements of wood-pastures relevant for biodiversity and these should be protected.

Zusammenfassung

Waldweiden sind empfindliche Ökosysteme, weil sie durch multifunktionale Bewirtschaftung geringer Intensität entstehen und davon abhängen. Auch wenn ihre ökologische und kulturelle Bedeutung hoch ist, verschlechtern sich der Zustand der Waldweiden in ganz Europa mit hoher Geschwindigkeit, überwiegend aufgrund von geänderter Landnutzung. Uns fehlt immer noch ein grundlegendes Verständnis des ökologischen Wertes der Waldweiden und der Eigenschaften, durch die sie sich von anderen

\*Corresponding author Tel.: +40 726 464 013; fax: +40 65 771375.
E-mail address: hartel.tibor@gmail.com (T. Hartel).

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Introduction

European wood-pastures are mosaic, structurally heterogeneous landscapes with high conservation value. Many contain a high number of protected species (Bergmeier, Petermann, & Schröder 2010), as well as keystone structures such as large, old trees (Manning, Fischer, & Lindenmayer 2006). Grazing is regarded as a key factor in creating and maintaining wood-pastures (Vera 2000; Gillet 2008). Traditionally, grazing co-occurred with the use and extraction of a wide range of tree-related goods and services, the most common being the fruit of trees and shrubs (e.g. acorn, pear, apple, rosehip) and wood (extracted e.g. by coppicing and pollarding) (Vera 2000; Bergmeier et al. 2010; Hartel & von Wehrden 2013; Rotherham 2013).

European wood-pastures went through dramatic changes in the past two centuries. A major driver of these changes was the increasing societal demand for timber and agricultural products. Often, the traditional extensive and multifunctional use of wood-pastures was unable to meet these growing demands, and was therefore replaced by more intensive, largely monofunctional forestry and agricultural practices (Vera 2000; Hartel & Plieninger 2014). Similar processes of increasing industrialization and specialization of agricultural production in response to growing demand have occurred throughout Europe (Bowler 1985), and as a result, many wood-pastures have been abandoned and reforested (Vera 2000). Grazing was separated from woodlands and restricted to pastures, which were specifically managed for livestock production, while forests were used for timber production (Hartel & Plieninger 2014).

Traditional wood-pastures have persisted in parts of Europe, especially in economically marginal regions, where land use has often retained many traditional features. However, land use changes are now imminent in these regions, including the possible expansion and intensification of arable fields, urbanization, road construction, land abandonment (and reforestation), logging, and uncontrolled pasture burning (Bergmeier et al. 2010; García-Jejeño, Taboada, Tárrega, & Salgado 2011; Hartel & von Wehrden 2013; Kizios, Plieninger, & Schaich 2013; Plieninger & Schaar 2008).

Regardless of the nature of these threats, the outcomes from the perspective of wood-pastures are typically the same: the heterogeneous environment maintained by multifunctional land use, characterized by woody vegetation and shrubs scattered through grassland, is transformed into either a closed forest or a treeless open landscape, providing a narrower range of ecosystem services and potentially supporting less diverse ecological communities.

Considering the rapid deterioration of the remaining wood-pastures across Europe, there is an urgent need to understand their characteristics, biodiversity, and historical and current management. A number of recent papers, mostly from Western, Central and Northern Europe, have explored the relationship between biodiversity and the (changing) management of wood-pastures (e.g. Schmucki, Reimark, Lindborg, & Cousins 2012; Chételat, Kalbermatten, Lannas, Spiegelberger, Wettstein 2013; Hevia, Azcárate, Oteros-Rozas, González 2013; Sebek, Altman, Platek, & Cizek 2013; Ramírez-Hernández, Micó, de los Ángeles García, Brustel, & Galante 2014). Taxonomic groups considered included lichens (Palto, Nordberg, Nordén, & Snäll 2011), insects (Silva, Aguiar, Niemelä, Sousa, & Serrano 2008; Taboada, Kotze, Salgado, & Tárrega 2010; García-Jejeño et al. 2011; Azcárate & Peco 2012; Streitberger, Hermann, Kraus, & Fartmann 2012), reptiles (Martín & Lopez, 2002; Godinho, Santos, & Sá-Sousa 2010), birds (Fonderflick, Caplat, Lovaty, Thévenot, & Prodon 2010; Robles, Ciudad, & Matthysen 2011), small mammals (Gonçalves, Alcobia, Simões, & Santos-Reis 2011) and bears (Roellig, Dorrestijn, von Wehrden, Harel, & Fischer 2014).
In this paper, we study the biodiversity value of wood-pastures in terms of bird diversity in a changing cultural landscape in Eastern Europe, namely in Southern Transylvania, Romania. Our study system provides a unique opportunity to understand how the traditional cultural and ecological environment has shaped biotic communities. First, rich historical records are available for our study region about the past management of treed landscapes (Dorner 1910; Orosz 2004; Hartel et al. 2013; Öllerer 2014), which provides a historical-cultural perspective. Second, Southern Transylvania harbors ‘historic landscapes’ (Akeroyd & Page 2006) whose overall level of woodland cover has changed relatively little during the centuries (Dorner 1910), suggesting a certain level of structural stability of these landscapes over time. Third, the region is rich in ancient wood-pastures (Hartel et al. 2013) and veteran trees (Hartel & Moga 2010). Old trees are considered keystone structures in ecosystems, and provide ecological continuity through time (Manning et al. 2006; Manning, Gibbons, & Lindenmayer 2009).

Fourth, parts of these historic landscapes have experienced considerable changes over recent decades. For example, many wood-pastures have been transformed into open fields or pastures. Open pastures are novel landscape structures for this region—traditionally, pastures in this region always contained trees (Stolcz 1907; Dorner 1910; Hartel et al. 2013). Moreover, the scattered old trees from the study region are rapidly disappearing because of logging, uncontrolled pasture burning, and changing grazing management favoring sheep instead of cattle (Hartel et al. 2013; Sutcliffe et al. 2014).

We selected passerine birds for our study due to their high diversity in species, behavioral and ecological traits. A number of papers have documented the importance of tree-related (such as tree size, density, hollows), woodland-related (cover, distance) and shrub-related variables for bird communities and individual species in various parts of Europe (e.g. Newton 1994; Orłowski 2005; Moga, Hartel, Öllerer, & Szapanos 2008; Moga, Hartel, & Öllerer 2009; Brambilla et al. 2010; Gonçalves et al. 2011; Reif, Marhoul, Čížek, & Konvička 2011; Robles et al. 2011; Wuczysiński, Kujawa, Dajdok, & Grzesiak 2011; Dorresteijn, Hartel, Hanspach, von Wehrden, Fischer 2013; Navedo et al. 2013).

First, as a general overview, we compared bird species composition and richness of wood-pastures, forests and open pastures using multivariate analyses and species accumulation curves. Second, we explored the relationships between variables describing wood-pastures and species traits of the passerine bird communities using RLQ and fourth corner analyses, to obtain a mechanistic understanding of how certain characteristics of wood-pastures relate to the presence of certain species and their specific characteristics. We show that wood-pastures are heterogeneous landscape elements that sustain a diverse bird community, which is distinctly different from those of open pastures or forests.

Materials and methods

Study area

The study area was situated in Southern Transylvania, Romania, and covered approximately 3600 km². The coordinates of the central locality, Sighișoara, are: N 46°13’07.69” E: 24°47’25.47” (with a relief of the central locality, Sighișoara, are: N 46°13’07.69”, E: 24°47’25.47”). The relief is hilly, with altitudes ranging from about 400 to 800 m. Detailed descriptions of the study area are presented by Fischer, Hartel and Kuemmerle (2012), Hartel and von Wehrden (2013) and Hartel et al. (2013). The region is dominated by traditional land use practices and infrastructure is poorly developed. Urban areas cover about 3% of the area, while major land cover types are forest (approx. 30% coverage), pasture (approx. 26%), heterogeneous agricultural area (agro-forestry systems included—about 15%) and arable fields (approx. 14%).

Previous work showed that forests and wood-pastures in the region differed in tree composition (forests dominated by hornbeam, Carpinus betulus and beech, Fagus sylvatica, wood-pastures dominated by oak Quercus robur and Q. petreae, and pear, Pyrus communis and P. pyraster), tree size (trees of the same species being larger in wood-pastures than in forests), and prevalence of dead trees (with more dead trees in forests) (Hartel et al. 2013). Moreover, tree density was higher in forests (typically >600 trees per ha) than in wood-pastures (typically <10 trees per ha) (Dorresteijn et al. 2013). Most forests are managed and have little understory, other than sparsely distributed tree seedlings. The prevalence of dead trees was higher in forests than in wood-pastures (Hartel et al. 2013).

Site selection and bird surveys

We surveyed birds in 41 wood-pastures, 15 closed forests, and 15 treeless pastures (hereafter ‘open pastures’) (Fig. 1). One sampling site (hereafter ‘site’) of 2 ha was situated in each of these locations. We sampled a larger number of wood-pastures than forests and open pastures because forests and open pastures are relatively homogenous, whereas wood-pastures differ substantially in structural elements and adjacent forest cover.

The selection of sampling sites is described below (see also Dorresteijn et al. 2013; Hartel et al. 2013). To assure that sampling points were independent, wood-pasture sites were separated from one another by at least 2 km, with one exception of 1.5 km. Minimum distances between forest and wood-pasture sites were typically at least 1.5 km, with one exception of 960 m. Open pasture sites were located at least 1.5 km from all other survey sites.

Within the wood-pastures, sampling sites were located centrally whenever possible. Forest sites were chosen on the basis of accessibility, and all sites were located 270–850 m from the forest edge. In the case of open pastures, we selected portions which contained no trees or shrubs within about
400–500 m around the survey point, and the minimum distance to the nearest forest edge was about 500 m.

Each site was surveyed twice for passerine birds in the breeding season in 2012: the first survey occurred between 10 April and 1 May, and the second one between 10 May and 18 June. The data from both surveys were combined for the analysis. Surveys were undertaken from sunrise until 11 am. under good weather conditions. Birds were recorded within a 2 ha circular site (80 m radius around a central point) for 10 min by combining visual and aural assessments. In the first 5 min birds were surveyed from the central point of the site (Bibby, Burges, Hill, & Mustoe 2000) and for the next 5 min the observer slowly walked within the 2 ha site in order to increase detectability. Species passing through the site were not recorded. Only presence data was used in the analysis.

Wood-pasture variables

Wood-pastures were characterized by 13 variables recorded at three spatial scales (see Table 1 for the variables and indications on how these were measured). The local scale was represented by the 2 ha site also used for bird surveys. The intermediate scale was represented by a 220 m buffer around the 2 ha site (i.e. up to 300 m from the center of the 2 ha site), and the landscape scale was represented by a buffer of 500 m around the intermediate buffer (i.e. up to 800 m from the center of the 2 ha site). In a given 2 ha site, we measured tree density per ha, density of dead trees per ha, percentage shrub cover, density of oak, hornbeam and pear per ha, and average size of all trees (Table 1). The variables used to characterize the intermediate scale were: tree density per ha, number of dead trees, percentage shrub cover and percentage forest cover (Table 1). The landscape scale was characterized by two variables: tree density per ha and percentage forest cover (Table 1).

Bird life history traits

Two life history traits were selected to characterize passerine birds. These were: diet (omnivorous, insectivorous and granivorous) and nest location (ground nester – open nest on the ground; shrub nester – open nest in shrubs; hollow nester – in our case in tree hollows; and open tree nester – open nest in a tree). The life history traits of each bird species for all three landscape types studied is shown in Appendix A. We used Cramp and Perrins (1993) and Wuczyński et al. (2011) for the above categorization, which was adapted to our field conditions and field experience (Moga et al. 2009).
Table 1. The variables used to explore the relationship between bird community structure and environmental features of wood-pastures (n = 41) with basic descriptive statistics.

<table>
<thead>
<tr>
<th>Variable name (code*)</th>
<th>Mean</th>
<th>SD</th>
<th>CV</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2 ha (site) level</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density per ha (Tree_dens_ha)</td>
<td>7.71</td>
<td>4.81</td>
<td>0.62</td>
<td>All standing trees (dead and alive) were counted in the field and divided by two.</td>
</tr>
<tr>
<td>Density of dead tree per ha (Dead_ha)</td>
<td>1.14</td>
<td>2.30</td>
<td>2.01</td>
<td>The number of dead trees (standing and fallen) was counted in the field and divided by two.</td>
</tr>
<tr>
<td>Shrub cover (Shrub 2 ha)</td>
<td>8.80</td>
<td>16.52</td>
<td>1.87</td>
<td>The percent of shrub was visually assessed in the field. We defined as shrub woody perennials (including young trees) being between about 0.3 m and 3 m (Hartel et al. 2013).</td>
</tr>
<tr>
<td>Oak tree density per ha (Quercus_ha)</td>
<td>4.47</td>
<td>3.65</td>
<td>0.81</td>
<td>The number of stems belonging to oaks (Quercus robur and Q. petraea pooled) counted in the field, divided by two.</td>
</tr>
<tr>
<td>Hornbeam tree density per ha (Carpinus_ha)</td>
<td>1.32</td>
<td>2.26</td>
<td>1.70</td>
<td>Calculated similarly as for oaks.</td>
</tr>
<tr>
<td>Pear tree density per ha (Pyrus_ha)</td>
<td>1.01</td>
<td>1.63</td>
<td>1.61</td>
<td>Two pear species (Pyrus communis and P. pyraster) pooled together. Calculated similarly as for oak and hornbeam.</td>
</tr>
<tr>
<td>Tree size (Tree(DBH))</td>
<td>75.41</td>
<td>17.88</td>
<td>0.23</td>
<td>Diameter at breast height in cm was measured for trees higher than 3 m in a given two hectare site and subsequently averaged for the whole wood-pasture.</td>
</tr>
<tr>
<td><strong>300 m (intermediate) buffer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density per ha (Tree_ha,300)</td>
<td>1.73</td>
<td>1.03</td>
<td>0.59</td>
<td>The number of scattered trees was counted based on all crowns discerned on Google Earth satellite image in the buffer between the margin of the 2 ha site and the 300 m. The tree density per ha was calculated from the area (ha) of this buffer.</td>
</tr>
<tr>
<td>Number of dead trees (Dead,300)</td>
<td>2.68</td>
<td>4.22</td>
<td>1.57</td>
<td>Counted along four 220 m long strip transects of about 10 m width starting from the margin of the 2 ha in the four cardinal directions (NWSE). A total number was calculated from these transects for each wood-pasture and this number was used to characterize the amount of dead trees in this buffer.</td>
</tr>
<tr>
<td>Shrub cover (Shrub,300)</td>
<td>7.90</td>
<td>10.13</td>
<td>1.28</td>
<td>The shrub was estimated visually along the four 220 m long and about 2 m width transects. It was expressed in meters of shrub cover (i.e. x m of shrub out of 220 m transect) and then this value was transformed to percentage. The percentages gathered from the four transects were averaged and the value was used as shrub cover for the 300 m buffer of each site.</td>
</tr>
<tr>
<td>Forest cover (Forest,300)</td>
<td>16.07</td>
<td>20.46</td>
<td>1.27</td>
<td>Percentage of forest cover of the 300 m buffer calculated from the margin of 2 ha site, based on the CORINE Land Cover Classes.</td>
</tr>
<tr>
<td><strong>800 m (landscape) buffer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density (Tree_ha,800)</td>
<td>0.39</td>
<td>0.30</td>
<td>0.77</td>
<td>Similarly as for the 300 m buffer (see above), but using the 300 m–800 m buffer. For the majority of the wood-pastures this number includes the majority if not all the trees in the wood-pasture and beyond.</td>
</tr>
<tr>
<td>Forest cover (Forest,800)</td>
<td>31.29</td>
<td>22.58</td>
<td>0.72</td>
<td>In percent, as for the 300 m buffer (see above).</td>
</tr>
</tbody>
</table>

SD, standard deviation; CV, coefficient of variation.
*code as used in the RLQ analysis.

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Data analysis

Data analysis involved two steps. First we compared the bird communities of wood-pastures with those of forests and open pastures to explore the potential differences between the three landscape types. Second, we explored the relationship between bird species traits and a number of environmental variables describing wood-pastures.

We used nonmetric multidimensional scaling (NMDS) to visualize the similarity of bird species composition in forest (F), wood-pasture (WP) and open pasture (P) sites. Because we used the presence/absence data, the dissimilarity between the sites was measured with the ‘Jaccard’ distance measure. The statistical significance of the difference in bird community composition between sampling units (i.e. forest, wood-pasture and open pasture sites) was tested using analysis of similarity (ANOSIM) with 10,000 permutations. These analyses were undertaken in R (R Development Core Team 2012) with the Community Ecology Package ‘vegan’. We computed species accumulation curves for wood-pasture, forest and open pasture sites to compare the species richness of their bird communities. If most of the species are rare (i.e. present in few sites) species accumulation curves increase steadily. Conversely, if many species are present in many sites, species accumulation curves can be expected to be steep at the beginning but then level off quickly (Thompson & Withers 2003).

We performed an RLQ analysis to explore the relationship between bird species traits and environmental variables describing wood-pastures. RLQ analysis uses three data matrices: a matrix with environmental variables and sampling sites (R), a matrix containing the presence/absence of species at each site (L), and a matrix with the species life history traits (Q) (Doledec, Chessell, ter Braak, & Champely 1996). As the first step, we calculated the variances of the separate ordination of each of these data matrices: we used principal components analysis (PCA) for R, correspondence analysis for L, and a Hill-Smith PCA for Q (Hanspach, Fischer, Ikin, Stott, & Law 2012). As a second step, we explored the joint structure of the three data matrices via RLQ analysis (Doledec et al. 1996). The total inertia values for the R and Q data matrices were also calculated. Inertia provides an index that shows the independence between two datasets. High inertia indicates strong links between the R and Q data matrices through the L matrix (Doledec et al. 1996). The significance of relationships between environmental variables and traits was tested using fourth corner analysis following Dray and Legendre (2008). Specifically, the fourth corner analysis assesses the links between all possible combinations of environmental variables and traits and then tests if those links are significantly stronger than it would be expected by chance. RLQ and fourth corner analyses were performed using the package ‘ade4’ in R (R Development Core Team 2012).

All environmental data were z-transformed prior to analysis. Descriptive statistics of the environmental variables describing wood-pastures are presented in Table 1.

Results

Bird community composition in forests, wood-pastures and open pastures

We recorded a total of 36 passerine bird species. Fourteen bird species were found in forests, four in open pastures, and 32 in wood-pastures (Appendix A). One species was recorded only in forest (Phylloscopus sibilatrix, at one site), three were found only in open pastures (Miliaria calandra, Motacilla flava, Saxicola rubetra), and 18 species were found only in wood-pastures (e.g. Emberiza citrinella, Anthus trivialis, Lanius collurio; see Appendix A for full species list). Fringilla coelebs was detected in all forest sites, while Sturnus vulgaris was found in all wood-pasture sites, and Alauda arvensis in all open pasture sites. The proportion of declining species according to the BirdLife International (2004) classification was 21% for forests, 31% for wood-pastures and 100% for open pastures. Closed forests lacked ground nester birds while open pastures had only ground nester species. Wood-pastures contained bird species belonging to four nesting traits (ground nesters, open tree nesters, shrub nesters and tree hollow nesters, Appendix A).

Mean species richness did not differ between forests and wood-pastures (mean forest = 7.13, 95% confidence interval = [5.94; 8.32]; mean wood-pasture = 6.12 [5.36; 6.88]), while open pastures had on average 1.20 ([0.92; 1.48]) species. Species spatial turnover was higher in wood-pastures than in closed forests and open pastures, regardless of whether these were considered separately or jointly (Fig. 2).

The bird communities of wood-pastures were statistically distinct from those of forests and open pastures (Fig. 3; ANOSIM statistic, R = 0.77, P < 0.0001). The difference between bird communities of wood-pastures and closed forests remained significant (ANOSIM statistic, R = 0.33, P < 0.0001) after removal of open pasture sites.

Environment-bird trait relationship in wood-pastures

The results of the RLQ analysis are shown in Fig. 4. The first axis explained 47% of the variance and the second axis 35% (Table 2). Shrub cover within the 2 ha site had the highest loading on axis 1, while oak and dead tree density and tree size within the 2 ha site had the highest loadings on axis 2 (Fig. 4). Ground nesters were plotted opposite to high shrub cover (Fig. 4). The fourth corner analysis showed a significant positive association between the hollow nesting bird.
species and the density of oak trees and large trees at the site level, the insectivorous birds and the density of pear trees at site level and the shrub-nesting birds and shrub cover at the site level. The ground nesters were significantly negatively associated with the shrub cover at site level ($P<0.05$ in all cases, Appendix B).

**Table 2.** Results of the $RLQ$ analysis of site related environmental variables ($R$), bird species composition ($L$) and bird traits ($Q$). Separate ordinations represented by the principal component analysis (PCA), correspondence analysis (CA) and the Hill-Smith PCA are also presented. Values for the separate ordinations and the $RLQ$ analysis represent the eigenvalues (% variance explained) of the first two axes.

<table>
<thead>
<tr>
<th></th>
<th>Axis 1 (%)</th>
<th>Axis 2 (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Separate ordinations</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R$ (PCA)</td>
<td>3.19 (24.55)</td>
<td>2.51 (19.32)</td>
</tr>
<tr>
<td>$L$ (CA)</td>
<td>0.38 (10.31)</td>
<td>0.36 (9.72)</td>
</tr>
<tr>
<td>$Q$ (Hill-Smith PCA)</td>
<td>1.52 (30.51)</td>
<td>1.19 (23.98)</td>
</tr>
<tr>
<td>$RLQ$ analysis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$RLQ$ axis eigenvalues</td>
<td>0.14 (47.22)</td>
<td>0.10 (34.68)</td>
</tr>
<tr>
<td>(total =0.31)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Correlation: $L$</td>
<td>0.25</td>
<td>0.18</td>
</tr>
<tr>
<td>Inertia: $R$</td>
<td>2.07</td>
<td>4.21</td>
</tr>
<tr>
<td>Inertia: $Q$</td>
<td>1.10</td>
<td>2.49</td>
</tr>
</tbody>
</table>

**Discussion**

We found differences between the passerine bird communities for wood-pastures, closed forests and open pastures. Moreover, we identified key structural elements of wood-pastures for the bird communities in wood-pastures. We discuss these findings in relation to the ecology of the bird...
species, but also in relation to the management history of landscapes in our study area.

**Bird communities in wood-pastures compared to closed forests and open pastures**

Wood-pastures had significantly different bird communities and higher total species richness than the closed forests and open pastures. Differences in community structure and richness in closed forests versus wood-pastures have been reported for birds (Smith, Burgess, & Parks 1992; Camprodon & Brotons 2006), small mammals (Gonçalves et al. 2011), and ground beetles (Taboada, Kotze, & Salgado 2010). Wood-pastures are ecologically heterogeneous environments. Scattered old trees and shrubs within the pasture (see Fig. 1B and C) provide important habitat for the tree, shrub- and grassland-related birds. Indeed, our study showed that all four nesting traits (i.e. nesting in shrub, nesting in tree hollows, building open nests in trees, nesting on the ground) were well represented in wood-pastures, whereas closed forests lacked ground nesting passerine species and open pastures lacked tree and shrub nesting species. The forests in our region are currently managed for timber production and have a high density of trees and a closed canopy (Dorresteijn et al. 2013; Hartel et al. 2013). Many of these forests were managed as silvopastoral systems in the past, grazed predominantly by pigs and later by cattle (Dorner 1910; Oroszi 2004), and were visualized as wood-pastures in historical military maps from the 18th and 19th centuries (TH personal observations). This suggests that at least some of the current closed forests (as shown in Fig. 1A) in our region are relatively new landscape structures, which emerged from previously more open wood-pasture systems when the multifunctional wood-pasturing management was changed into the modern forestry and pasturing (Oroszi 2004). It is likely that these changes represented “environmental filters” (Hanspach et al. 2012) which excluded some passerine bird species and life history traits, thereby changing bird community structure. It was shown for example that the ecological conditions determined by tree canopy structure significantly influence bird communities in European woodlands (Hinsley, Hill, Fuller, Bellamy, & Rothery 2009). On the other hand, the complete elimination of woody vegetation from wood-pastures (Fig. 1D) has resulted in the elimination of species depending on shrubs and trees, while ground nesters such as the skylark were favored. Since the forest sites had a more balanced proportion of hornbeam, oak and beech while the wood-pasture sites were dominated by oak (Hartel et al. 2013), this may have a role in determining the differences in the passerine bird communities. However, we believe that configuration variables, such as the density of trees and the canopy cover, rather than tree species composition, were the main driver of the bird species in our system. This is supported by the fact that all but one bird species that were found in the closed forests were also present in the wood-pasture sites (see Results) and that a number of open habitat (farmland) birds were present only in the wood-pasture sites (Appendix A).

**Bird communities in wood-pastures**

The functional traits of birds in wood-pastures were related to shrub cover (positively for shrub nesters and negatively for ground nesters), oak density (hollow nesters), pear density (insectivorous birds) and tree size (hollow nesters). All these structural elements of wood-pastures were highly valued by the traditional communities from our region for the various goods and services they provided (Hartel et al. 2013). For example oaks were selectively maintained for the shadow
and acorn they provided for livestock, as well as for their overall positive effects on the pastures (especially in extreme dry summers). The largest trees from the region covered by our study are the oaks from wood-pastures (Hartel et al. 2013). Pear trees were maintained (and planted) for their fruits (which served as food for livestock and people, as well as source for alcoholic drinks) and their role against soil erosion. Many pear trees were planted in the past two centuries (Oroszi 2004). Some shrubs were also retained in every wood-pasture for their fruits (Hartel et al. 2013). Traditional wood-pastures always contained some shrubs, and large trees at various densities, due to the multifunctional nature of their management.

The value of large trees, fruit trees and shrubs habitat elements for passerine birds have been shown by many other studies. For example, it is well known that the hollow nester birds may be limited by the availability of tree cavities, which in turn are associated with large, dead trees (reviewed by Newton 1994). By contrast, when dead trees and hollow trees are present at high densities in most of the sites, their relative importance to other habitat elements will be lower (see e.g. Dorrestein et al. 2013 for woodpeckers and Smith et al. 1992 for woodland birds in general). Pear trees were important for insectivorous birds. The most likely explanation for this association is that the fruit trees with sweet fruits such as the pear and apple are attractive for invertebrates, particularly insects which in turn will attract the insectivorous birds (Mols & Visser 2002; Simon, Bouvier, Debras, & Sauphanor 2010; Myczko et al. 2014). Shrub cover at site level was important for shrub nesters. Typically, a moderate level of shrub cover positively influences the occurrence and species richness of birds (e.g. Orłowski 2005; Telleria 2008; Brambilla et al. 2010; this study). The abandonment of wood-pastures after the collapse of Romanian communism (1989) resulted in the increase of shrub cover (Fig. 1C) and the persistence of dead tree elements in some wood-pastures, which would be otherwise have been removed (Hartel et al. 2013). This situation may represent an important momentum for conserving these keystone structures for biodiversity.

Conclusions and conservation implications

In this study we showed that wood-pastures harbor a rich and unique bird community, which is more diverse than the combination of the bird communities of forests and open pastures. Structural elements such as the large trees, oak and pear trees and the shrubs were important for birds. In most European wood-pastures the high diversity of ecological conditions has been traditionally related to multifunctional extensive landscape management combined with the selective maintenance (or even enrichment) of certain tree species (e.g. oak and pear, Hartel et al. 2013). Specialization in commodity production, in contrast, has resulted in a shift from multifunctional to monofunctional landscape management. Many trees (such as the pear and oaks) were removed from wood-pastures of Central Europe in the past decades due to the adoption of more intensive pasturing systems (Bergmeier and Roellig 2014; Oppermann 2014). This has resulted either in the formation of closed forests or in open landscapes that often lack woody vegetation and shrubs. We showed that these forest and open landscapes have bird communities that are distinct from those occurring in the wood-pastures. Although they are different from wood-pastures, forests and pastures also can have significant ecological value. For example, our study showed that both closed forests and open pastures can provide habitat for birds which are declining in the European Union. Both closed forests and open pastures can be managed for biodiversity, especially via the pro-active retention or introduction of structural elements that benefit biodiversity (e.g. some shrubs, dead trees, small wetlands). However, the management of wood-pastures for biodiversity requires special attention. Biodiversity conservation in wood-pastures is inextricably linked to the management (and cultural) history of these systems, as well as the ecology of the organisms inhabiting them (see also Ramírez-Hernández et al. 2014 for the ‘dehesa’ systems regarding insect groups). We showed that oak and pear trees as well as the large trees are important for hollow nester and insectivorous birds. Besides their ecological value, these trees are important elements of the cultural heritage of this region, being maintained by the rural societies for their various services. National and European Union level legislations and policies should recognize wood-pastures as unique, multifunctional landscapes with high ecological and cultural value and to promote their use as such. Maintaining shrubs, large, often dead trees and fruit trees in pastures, combined with traditional grazing would contribute to the ecological and cultural value of these systems. The success of a Europe-wide conservation strategy for wood-pastures will lie in the formal recognition in relevant policy documents of this landscape element and its major biodiversity values.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2014.06.007.

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