



Analysis

The importance of species diversity for human well-being in Europe

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ABSTRACT

Nature affects human well-being in multiple ways. However, the association between species diversity and human well-being at larger spatial scales remains largely unexplored. Here, we examine the relationship between species diversity and human well-being at the continental scale, while controlling for other known drivers of well-being. We related socio-economic data from more than 26,000 European citizens across 26 countries with macroecological data on species diversity and nature characteristics for Europe. Human well-being was measured as self-reported life-satisfaction and species diversity as the species richness of several taxonomic groups (e.g. birds, mammals and trees). Our results show that bird species richness is positively associated with life-satisfaction across Europe. We found a relatively strong relationship, indicating that the effect of bird species richness on life-satisfaction may be of similar magnitude to that of income. We discuss two, non-exclusive pathways for this relationship: the direct multisensory experience of birds, and beneficial landscape properties which promote both bird diversity and people's well-being. Based on these results, this study argues that management actions for the protection of birds and the landscapes that support them would benefit humans. We suggest that political and societal decision-making should consider the critical role of species diversity for human well-being.

1. Introduction

Over the past decades a substantial body of research has highlighted the positive effects of nature on human well-being (e.g. Hartig et al., 2014; MA, 2005; Russell et al., 2013; Sandifer et al., 2015). The Inter-governmental Science-Policy Platform for Biodiversity and Ecosystem Services (IPBES) has named these benefits and services Nature's Contributions to People (NCP) (Díaz et al., 2018). According to the IPBES framework and the NCP concept, nature affects the material (e.g. food and building material) and non-material (e.g. physical and psychological health, inspiration and spirituality) aspects of human livelihood, and is a key factor in regulating important environmental processes (e.g. air

and climate regulation) (Díaz et al., 2015; IPBES, 2014). Of these three types of NCP, non-material NCP or services with no obvious material benefits may be the most difficult to study, especially as they are, by definition, intangible and subjective (Chan et al., 2012), and difficult to conceptualize (Fish et al., 2016; Satz et al., 2013). However, knowledge generated from research on non-material NCP is important because it may provide complementary information for natural resource management and policy decisions that are otherwise largely based on material NCP (e.g. Adams and Morse, 2019).

A number of indicators are available as measures of non-material NCP (e.g. Hernández-Morcillo et al., 2013; Sterling et al., 2017; Zorondo-Rodríguez et al., 2016). Several studies have investigated non-

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material NCP by using subjective measures of well-being such as life-satisfaction or subjective health measures. City residents, for instance, living close to urban green space such as parks exhibit higher levels of life-satisfaction (Bertram and Rehdanz, 2015; Krekel et al., 2016; White et al., 2017). Within cities and beyond, studies also show that good access to vegetated areas is related to better cognitive function and development (Bratman et al., 2012; Reuben et al., 2019), fewer symptoms of depression (Cohen-Cline et al., 2015; Miles et al., 2012), lower self-reported stress (van den Berg et al., 2010) and lower risk of psychiatric disorders (de Vries et al., 2016; Engemann et al., 2019).

While these studies use a variety of indicators to examine human well-being, they have used a very limited set of indicators to describe nature. For instance, many studies mainly focus on the extent (e.g. size, total area cover) or proximity to water bodies (e.g. lakes, rivers) and vegetated areas (e.g. natural areas, urban parks), also termed blue or green space (Gascon et al., 2015; Völker and Kistemann, 2011; World Health Organization, 2017). More recently, studies have explored links between biodiversity, non-material NCP and human well-being (e.g. Lovell et al., 2014; Marselle et al., 2019; Sandifer et al., 2015), but few have made use of ecological measures of species diversity (e.g. based on field sampling and monitoring) as indicators for biodiversity.

Using such species diversity measures, a recent study demonstrated that faunal and floral species richness (number of species) is positively related to the subjective well-being of residents in the State of Victoria, Australia (Mavoa et al., 2019). Higher plant species richness is also positively associated with people's ability to recover from stress (Lindemann-Matthies and Matthies, 2018) while composite measures of multi-taxa species richness (plants, birds and bees/butterflies) are related to restorative benefits of urban parks (Wood et al., 2018). Other studies show positive relationships between bird and plant species richness and psychological well-being in urban parks (Fuller et al., 2007), although results are not always consistent (Dallimer et al., 2012). Furthermore, bird species richness and abundance are linked to personal and neighborhood well-being (Luck et al., 2011) and afternoon bird abundance is associated with better mental health in urban residents (Cox et al., 2017). These studies provide valuable insights on how humans can benefit from species diversity and argue that positive effects can be attributed to the fact that people enjoy watching and interacting with birds (Belair et al., 2015; Cox and Gaston, 2016), or that they appreciate the aesthetic value of plant diversity (Hoyle et al., 2017; Lindemann-Matthies et al., 2010; Southon et al., 2017).

Despite recent efforts to study the non-material influence of species diversity on different measures of human well-being, several open questions remain. First, most of the studies were conducted on a small spatial scale such as urban parks or urbanized areas. In comparison, our knowledge about the effect of species diversity on human well-being on a larger spatial scale is still very limited (but see Wheeler et al., 2015, for a national study in the UK). Second, to our knowledge, researchers have not yet investigated the effect of species diversity on life-satisfaction as an indicator for human well-being. However, an assessment of the large-scale relationship between species diversity and life-satisfaction may help us to understand if observed local-level patterns can be generalized beyond the specific local setting and are also evident on larger spatial scales while including a wider range of species numbers (diversity) and non-urban residents, who may have a different relationships with species diversity. Analyses of such large-scale relationships may also enable us to conduct comparisons between countries or regions, highlight research needs and provide knowledge on non-material NCP that can inform national and regional policy and management decisions.

The aim of this study is therefore to examine the relationship between species diversity and life-satisfaction on a continental level, focusing on multiple species groups and accounting for the potentially confounding effects of other nature characteristics and socio-economic factors. In our analyses, we relate life-satisfaction scores and socio-economic data of more than 26,000 European citizens from 26 countries with macroecological data on the regional level for species

diversity and other nature characteristics. Species diversity is measured as the species richness of birds, mammals (including megafauna) and trees. In addition, we compiled indicators for other nature and climate characteristics such as landscape and topographic heterogeneity, the area of green and blue space, or protected area cover.

2. Empirical approach

The assessment of people's self-reported life-satisfaction as a measure of subjective well-being has undergone critical evaluation (Kahneman et al., 1997; Kahneman and Krueger, 2006) and the conceptual underpinnings of using such data as a tool for preference elicitation and non-market valuation have been extensively discussed (Welsch, 2020; Welsch, 2009; Welsch and Ferreira, 2014). In recent years the approach has increasingly been used for preference elicitation and non-market valuation of environmental amenities and disamenities (for a recent review see Maddison et al., 2020). All of these studies established that subjective well-being is positively related to environmental quality and negatively related to environmental disamenities.¹

2.1. The econometric model

To assess the relationship between species richness and life-satisfaction we extended the general econometric model approach used previously (e.g. Ferrer-i-Carbonell and Frijters, 2004) to include species richness measures²:

$$LS_{ijr} = \alpha + \beta \ln(Y_i) + \gamma X_i + \delta G_j + \varphi \ln(D_j) + \eta N_j + \tau_r + \varepsilon_{ij} \quad (1)$$

where LS_{ij} represents self-reported life-satisfaction of individual i in NUTS region j . NUTS regions represent an EU classification of spatial units for Europe (French: *Nomenclature des unités territoriales statistiques*). Y_i is reported household income of individual i , X_i is a vector of demographic and socio-economic variables of individual i , G_j is a vector of geographical variables, D_j represents a vector of species richness measures, N_j is a vector of other nature and climate characteristics, and τ_r symbolizes country dummies (several NUTS regions j can be grouped within a country). The variables G_j , D_j and N_j were all measured at the NUTS regional level. The error term is represented by ε_{ij} , and β , as well as the vectors γ , δ , φ and η .

Various assumptions about the functional form of the econometric model are worth discussing. Following empirical findings regarding the functional form of income, household income is introduced into the model with its natural logarithm. Similar to the other nature characteristics, species richness measures were calculated on the NUTS regional level in the econometric model. Initially, we considered different specifications of species richness including linear and log-linear (natural logarithm) but the results presented focus on the log-linear specification of species richness of different taxonomic groups to account for a diminishing marginal utility at higher species richness values. Results from models with the linear specification are included in the supplementary information (Supplementary Tables S10-13).

3. Material and methods

3.1. Socio-economic data

Life-satisfaction and socio-economic data were derived from the 2012 European Quality of Life Survey (EQLS) with data for several thousand individuals ($n = 43,636$) from 34 European countries and 330

¹ This included a considerable range of environmental (dis)amenities such as air pollution, airport noise, green space, natural disasters and climate parameters. For a recent overview of the literature see Maddison et al. (2020).

² See e.g. Ferrer-i-Carbonell and Frijters (2004).

NUTS regions, with 1 to 38 NUTS regions per country due to their variable size (see summary statistics in Supplementary Table S3), as NUTS regions are classified according to average population size and existing administrative units.³ In the EQLS, most NUTS regions are categorized as NUTS 2 regions, but the data for Great Britain and France are on the NUTS 1 level while data for Lithuania and Latvia are on NUTS 3 level. EQLS data for Luxembourg, Cyprus, Croatia, Macedonia, Malta and Estonia were grouped on the NUTS 0 level, because either NUTS 1 or NUTS 2 levels were not clearly defined, or macro-economic data was only available at the national level (see below). The EQLS interviews were carried out by GfK Belgium between 2011 and 2012 with people aged 18 years and older. For more information see www.eurofound.europa.eu; data are offered by the UK Data Archive (University of Essex, Colchester, January 2014, 2nd Edition).

In the EQLS, information on life-satisfaction is obtained by asking individuals the following question: “All things considered, how satisfied would you say you are with your life these days?”. Respondents can choose from an ordinal scale of 1 to 10, where 1 means very dissatisfied and 10 means very satisfied. For our analysis, we included demographic and socio-economic explanatory variables from the EQLS at the individual level that have previously been found to have both positive and negative significant effects on life-satisfaction: income, age, gender, type of residential area (urban or rural), education level, health status, household structure/ marital status, employment status and volunteering behavior (Dolan et al., 2008; Meier and Stutzer, 2008). A quadratic term of age is also included, to account for the reported U-shaped relationship between age and life satisfaction (e.g. Dolan et al., 2008; Frey and Stutzer, 2002). Information on respondents’ monthly net household income is measured in income categories (e.g. the first category delimits a net monthly income <50 EUR). Based on the categorical income variable we calculated the mean of each income category ($n = 22$) in order to create a continuous income variable (e.g. to the lowest income category we assigned an income value of 25 EUR) (see Supplementary Table S1). We also accounted for the likelihood of a person experiencing green space by using data from a 5-item question in the EQLS which describes how the survey participants assess their access to recreational areas (e.g. sport facilities) or green space. We term the variable ‘Recreation Access’ and its five categories are: access with (1) great difficulty, (2) with some difficulty, (3) easily, (4) very easily and (5) service not used.

Additionally, we added macro-economic indicators at the NUTS level, in particular GDP, population density and unemployment rate as explanatory variables to the models. Data were available from the year 2011 at the NUTS 2 level by Eurostat (<http://ec.europa.eu/eurostat/>); data for Luxembourg, Cyprus, Macedonia, Malta and Estonia were often available only on country level. When values for 2011 were missing we used values from the year before or after (data for Serbia and Kosovo was not available) and when data for a specific region was missing, we calculated the average across lower-level NUTS regions (e.g. Croatia, France and UK). We calculated the size of each NUTS region to account for the different area sizes in the data analyses. Further, we added a binary variable termed “Eastern Europe” for all former European socialist countries (i.e. Latvia, Lithuania, Estonia, Poland, Czech Republic, Slovakia, Hungary, Romania and Bulgaria), since economic development and life-satisfaction in Eastern Europe, especially in former parts of the USSR and countries of the Warsaw Pact, is on average much lower compared to Western Europe, even accounting for confounding variables (Bonini, 2008). We do not report results for population density because we excluded this variable from our statistical models due to high correlations with green space area cover. Still, our analyses accounts for population characteristics to a certain degree as we include

³ NUTS level 1 regions are the largest (3–7 million people), NUTS level 2 an intermediate (0.8–3 million people), and NUTS level 3 areas the smallest spatial unit (150–800 thousand people). The three NUTS levels are spatially nested.

information on individual’s urban residency (see also Wheeler et al., 2015) with a binary variable termed “Urban” (1 = urban residents, 0 = rural residents).

3.2. Species richness, nature characteristics and climate

We compiled data on species richness, other characteristics of nature and climate for Europe from spatial data (atlas data or species distribution maps) and satellite imagery. For all data, except for data on green space, blue space and protected areas, we calculated variables by first compiling values on a European Universal Transversal Mercator (UTM) 50 × 50 km grid (see European Breeding Bird Atlas; EBBA). We then calculated the area weighted mean of these variables for each NUTS region (Table 1). This was done by weighting each variable value in a 50 × 50 km grid cell, which overlaps a specific NUTS-region, with the percentage of area shared by the grid cell and the NUTS region. For the data on green space, blue space and protected areas we calculated the percentage cover within the NUTS region (Table 1). The data for species richness, nature characteristics and climate were merged with the socio-economic data by using NUTS regions as matching ID. Our final data set contains two types of data, life-satisfaction and socio-economic data at the level of interviewed individuals, and species richness, nature characteristics, climate and the macro-economic variables at the level of the NUTS region which the individual inhabits.

3.2.1. Species richness

We use species richness as species diversity measure and calculated this variable for four species groups: birds, mammals, megafauna and trees (Table 1). We selected species groups for which a positive effect on humans has been demonstrated in local scale studies and for which species distribution data are available at the European scale. As data on European plant species distribution is not yet available, we used data on tree species richness.

Bird data was obtained from the first European Bird Census Council’s (EBCC) European Breeding Bird Atlas (EBBA) (Hagemeijer and Blair, 1997) (www.gbif.org, DOI:10.15468/adtfvf, accessed April 2017). The atlas data is available on a 50 × 50 km UTM grid map and contains information about the presence (“probable” and “confirmed” breeding records) and absence of 486 European breeding bird species collected mainly from 1980 to 1990. The temporal mismatch of the sampling periods between the EQLS and the EBBA atlas data should not be a major issue for this study because there have not been any major changes in species richness over time at the spatial scale of this study across Europe and within European countries (Koleček et al., 2010; Van Turnhout et al., 2007). Changes have mainly been observed for bird abundances (e.g. population numbers) within agricultural landscapes or in species community composition (Bowler et al., 2019; Reif et al., 2013; Le Viol et al., 2012). We provide additional analyses supporting these arguments in the supplementary information (Fig. S1, Supplementary Tables S14 & S15).

The EBBA data contains grid values of somewhat variable data quality across Europe (Hagemeijer and Blair, 1997). We dealt with the variable data quality by compiling two different versions of the bird atlas, one original data set that contains all grid cells and one data set where low quality grid cells, as identified in the EBBA (Hagemeijer and Blair, 1997), were defined as missing ($n = 219$, 3.7%). Based on both versions of the EBBA two variables for area weighted mean bird species richness were calculated for each NUTS region and then used in the analyses. Here (Figs. 1–3, Supplementary Tables S6–S13), we report only the results for bird species richness based on the original EBBA data set because the statistical models for the two species richness measures yielded the same overall results.

Information on mammal and megafauna species distribution in Europe was obtained from global IUCN range maps retrieved from the IUCN Red List data portal (www.iucnredlist.org, accessed 16 December 2016). We treated the IUCN presence categories ‘extant’, ‘probably

Table 1
Description of independent variables for species richness, nature characteristics and climate.

Main Category	Subcategory	Indicator	Literature
Species richness	Bird species richness	Area weighted mean species richness in NUTS region.	(Huby et al., 2006)
	Mammal species richness (all species)	We tested two bird data sets, one original data set with bird species richness values of all 50 × 50 km grid cells, and a second data set for which grid cells with low data quality were removed.	
	Mammal species richness (no bats)		
	Megafauna species richness (>44 kg)		
	Megafauna species richness (>0.5 kg)		
	Tree species richness		
Other nature characteristics	Landscape heterogeneity	Area weighted mean Shannon Diversity for land cover types in NUTS region. We used two classifications of land cover types, one with 5 and one with 15 land-cover classes (for classification see Supplementary Table S2)	(Wheeler et al., 2015)
	Topographic heterogeneity	Area weighted mean elevational range and standard deviation in elevational range in NUTS region	(Wilson and Gallant, 2000)
	Green space	Area covered by vegetated areas in NUTS region (%): green space was defined as arable land, permanent crops, pastures, heterogeneous agricultural areas, forests or scrub and/or herbaceous vegetation	(Krekel et al., 2016; Maas et al., 2008; White et al., 2017, White et al., 2013b)
	Blue space	Area covered by water bodies in NUTS region (%): blue space was defined as inland and marine waters	
	Coastline	Coastline dummy variable describing which NUTS regions have a coastline.	(Kopmann and Rehdanz, 2013)
Climate	Protected area cover	Area covered by Natura 2000 sites in NUTS region (%)	(Huby et al., 2006)
	Heating and cooling degree days (HDD and CDD)	Area weighted mean HDD and CDD in NUTS region	(Maddison and Rehdanz, 2011; Spinoni et al., 2015)

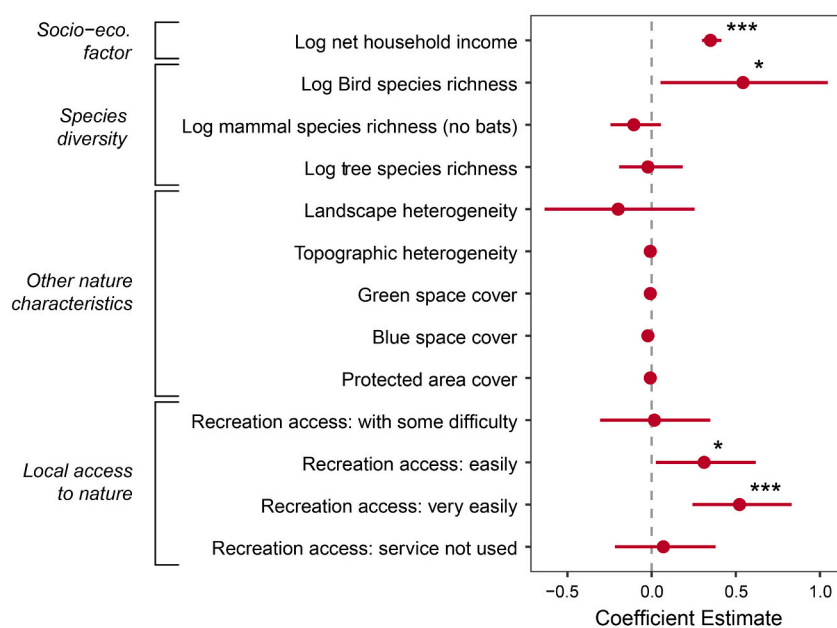


Fig. 1. Effect of socio-economic factors, species richness (log transformed), other nature characteristics and access to recreation areas on life-satisfaction across Europe. We show the coefficients of an OLS model (with clustered standard errors) for a selected set of explanatory variables and report the complete OLS model results in the Supplementary Table S6. 95% confidence intervals are depicted as error bars. For a more detailed description of the statistical analysis, see Methods and the Supplementary Information. AIC = 109,859.6; BIC = 110,408.6; LogLik = -54,862.8; Adjusted r-squared = 0.24. Asterisk symbols: **p* < 0.05; ***p* < 0.01; ****p* < 0.001.

extant' and 'possibly extant' as presences and then determined the area weighted mean species richness of all mammal and megafauna species. We wanted to account for the diverse ways humans might perceive and respond to different mammal taxa; we hence calculated species richness for different mammal groups. We considered (1) all mammal species, and (2) all mammal species excluding bats, which comprise a significant proportion of mammal diversity. We assume that bats are less noticeable to people because they are mainly active at night. For megafauna, we defined two variables based on body size measures (Jones et al., 2009), (1) mammals with a body mass larger than 44 kg, and (2) mammals with a mass larger than 0.5 kg. Mammals with a mass > 44 kg have been defined as megafauna (Barnosky, 2008; Doughty et al., 2016) and are often described as charismatic, especially in wildlife or ecotourism (Lindsey et al., 2007; Skibins et al., 2013). To consider also the fact that many species with medium body size (e.g. fox, hare) are also

appreciated by humans (e.g. Bell et al., 2017; Folmer et al., 2019), we additionally defined megafauna as mammals with an adult body mass larger than 0.5 kg.

Tree species distribution data was obtained from Mauri et al. (2017). This EU-Forest dataset includes a total of 588,983 occurrence records for 242 tree species across Europe (not including Iceland, Turkey and Macedonia). For each 50 × 50 km grid cell, we identified the tree species occurrences that lay within a grid cell and compiled the total number of forest tree species per grid cell.

We examined how much our species richness data varied within NUTS regions and determined for each species group whether the within-region variance of species richness was a major factor explaining the overall variation of species richness across Europe (between-region variance). For this purpose, we took species richness values from the 50x50km grid intersecting with the NUTS regions and performed simple

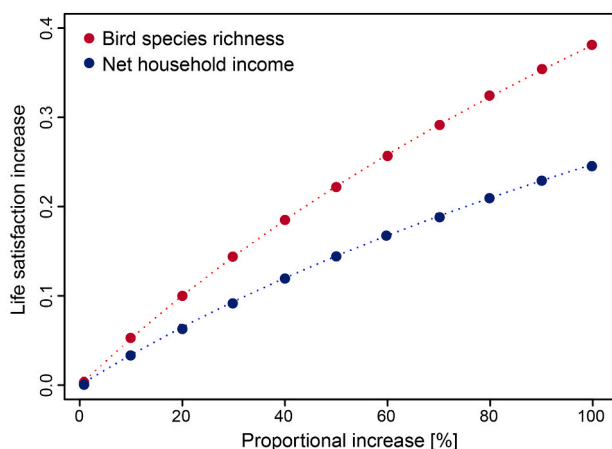


Fig. 2. Estimated life-satisfaction increase in relation to bird species richness and income. Estimates are based on the coefficients for log-transformed mean bird species richness and log-transformed net household income obtained from the OLS model (Fig. 1). In the OLS model we correct for socio- and macro-economic factors.

ANOVAs with species richness as the response variable and the NUTS regions as predictor variable. We only used species richness values (intersecting grid polygons) that covered at least 1% of the NUTS region area (max. of 66 values within a NUTS region, median = 11). Based on the ANOVA results we then calculated the percentage of overall variance across Europe explained by the within- and the between-region variation (NUTS region) by dividing the between-regions and residual sum of squares with the total sum of squares.

3.2.2. Other nature characteristics

Beside species richness we also used data for the following nature characteristics: landscape heterogeneity, topographic heterogeneity, green and blue space area cover, the presence or absence of coastlines and protected area cover (Table 1).

We selected variables reflecting landscape heterogeneity, because

people prefer heterogeneous landscapes for recreation (Paracchini et al., 2014) and because heterogeneous landscapes are often viewed as providing scenic views (Schirpke et al., 2013). To estimate landscape heterogeneity for each NUTS region we used data on land cover from the Coordination of Information on the Environment (CORINE) Land Cover database that provides land cover for the year 2012 in 44 land-cover categories as raster data (250 m resolution). We calculated landscape heterogeneity based on two different CORINE land cover classifications: one with 5 and the other with 15 aggregated land cover categories (see Supplementary Table S2). First, we determined the number of raster data points per land cover type within each 50 × 50 km grid cell. We then calculated for both land cover classifications the Shannon-Diversity Index for each grid cell. Both landscape heterogeneity variables were strongly correlated and performed similar during our analyses. We hence report results only for the classification based on 15 land-cover classes.

As additional measure of landscape heterogeneity, we used topographic heterogeneity. Topographic heterogeneity and elevation have been identified as indicators for landscapes with high recreational and aesthetic value (Peña et al., 2015; Sherrouse et al., 2011) or scenic views (de Almeida Rodrigues et al., 2018). We calculated the elevational range (meters) and standard deviation of the elevations within each 50 × 50 km grid based on a global digital elevation model (GTOPO30, 30 arc sec resolution) provided by the US Geological Survey (<https://earthexplorer.usgs.gov/>). Again, due to strong correlation and similar performances of the two variables, we used in further analyses only one variable, i.e. topographic heterogeneity calculated as area weighted elevation range.

In addition, we calculated the percentage of area covered by vegetated areas (green space) and water bodies (blue space) within each NUTS region using CORINE data. Green space and blue space have both been reported to have a positive effect on human well-being (Krekel et al., 2016; Völker and Kistemann, 2011). We defined green space as CORINE categories representing green vegetation and blue space as inland and marine waters (Table 1). We calculated the amount of green and blue space as the proportional area cover for each NUTS region. As an additional indicator for blue space, we created a binomial variable which describes whether a NUTS region has a coastline or not.

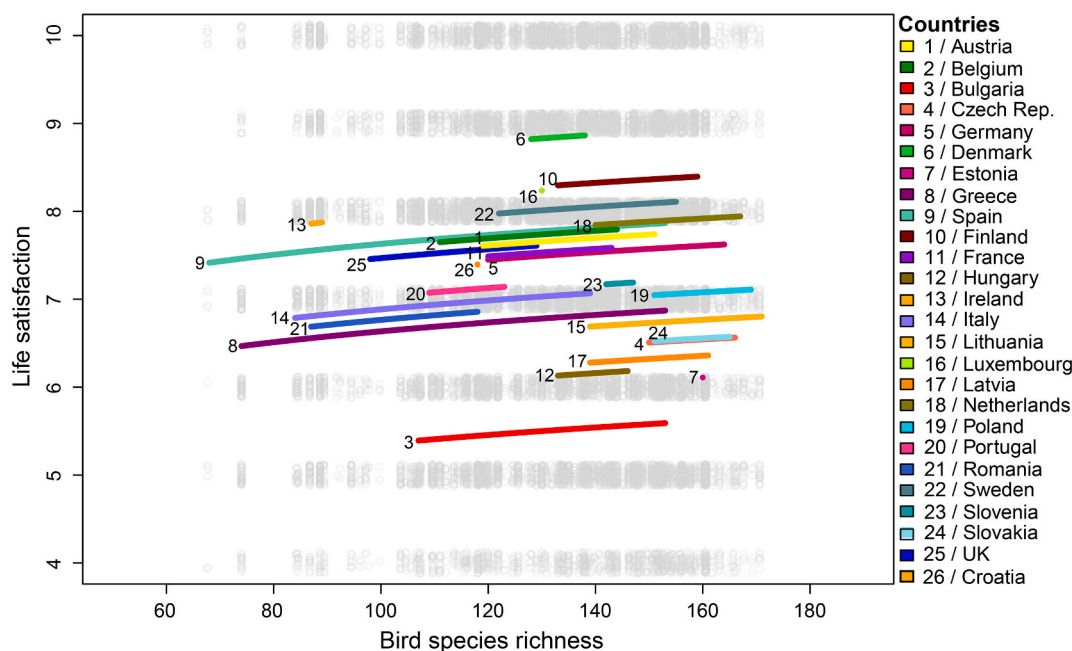


Fig. 3. Predicted range of life-satisfaction and bird species richness relationships across 26 European countries. Predicted values of life-satisfaction show a positive relationship between bird species richness across European countries (coloured lines). The length of each coloured line is equivalent to the range between minimum and maximum bird species richness in each country. Grey points in the background represent the raw data for life-satisfaction and bird species richness.

As indicator for high nature conservation value of the landscape, we calculated the percentage area covered by protected areas within each NUTS region. We defined as protected areas the Natura 2000 sites using information from the European Environmental Agency (EEA) (Nature 2000 sites, version 2016), and calculated the proportional area covered by terrestrial Natura 2000 sites (in percent) for each NUTS region.

3.2.3. Climate

A number of different ways of representing the climate have been considered in the subjective well-being/life-satisfaction literature (see Maddison and Rehdanz, 2020 for a recent overview). These include maximum and minimum monthly values for temperature and precipitation, as well as annual averages and counts of hot and cold and wet and dry months. It is argued that the use of deviations (HDD or CDD) is preferred to e.g. the use of maximum and minimum values because such a specification fails to distinguish between those locations where the temperature in the coldest month is already high, and those locations where the temperature in the hottest month is still quite low (Maddison and Rehdanz, 2020). We follow this line of reasoning and use cooling-degree days (CDD) and heating degree-days (HDD).

To calculate average CDD and HDD for the past 30 years we used the E-OBS climate data set (Haylock et al., 2008) (www.ecad.eu), a European land-only gridded climate raster data set (0.25 degree resolution) for the period of 1st January 1950–31st August 2016 (version 14). For our calculations of CDD and HDD we used the daily mean temperature data (T_M) from 1982 to 2012 and a base temperature (T_b) of 22 °C for CDD and 15.5 °C for HDD (Spinoni et al., 2015). In a first step, CDD and HDD were computed for each climate raster point by estimating the deviation (positive deviation = CDD, negative deviation = HDD) of T_M from the baseline temperature (T_b) and summarizing the results across all days within the 30-year period (1 Jan. 1982–31 Dec. 2012 = 11,322 days). We then divided the summarized values by 30 to obtain annual averages of CDD and HDD per climate raster grid cell. Subsequently, we calculated mean CDD and HDD for each 50 × 50 km grid cell and then the area weighted mean of CDD and HDD for each NUTS region. As both variables were strongly correlated, we selected only one of them, i.e. CDD for further statistical analyses.

3.3. The estimation procedure

Our final data set contains information for 26,749 individuals living within 228 NUTS-regions and 26 different countries after removing missing values⁴ (summary statistics can be found in Supplementary Tables S3, S4). We used linear regression models (ordinary least squares, OLS) and assumed cardinality of the life-satisfaction values as it provides greater flexibility in the use of parametric approaches to analyze life satisfaction (Kubiszewski et al., 2018). We are aware of different arguments for and against the assumption that life-satisfaction values are continuous (Ferrer-i-Carbonell and Frijters, 2004; Kristoffersen, 2017; Kromrey and Rendina-Gobioff, 2003; Ng, 1997). However, it has been shown that assuming ordinality or cardinality of the response variable makes little difference when studying life-satisfaction (Ferrer-i-Carbonell and Frijters, 2004). In addition, a recent study demonstrated that it is possible to make a cardinality assumption because life-satisfaction scores are equidistant, thus supporting cardinal comparability (Kristoffersen, 2017). We include results of the ordered logit specification for comparison that show our results are robust (Supplementary Tables S7, S9, S11 & S13).

Because our data set combines data on the individual and the NUTS level, we needed to account for possible impairments. For instance, in OLS models the hierarchical structure of the data could cause

⁴ Due to missing species diversity and macro-economic data we could not include the following countries in our analyses: Turkey, Iceland, Malta, Cyprus, Montenegro, Macedonia, Serbia, Kosovo.

correlations within groups of individuals living in the same NUTS region producing faulty standard errors. For this reason, we applied clustering at the NUTS level in the OLS regression, which relaxes the assumption that observations are independent and adjusts standard errors for intra-regional correlation (Moulton, 1990). With this procedure, heteroscedasticity-robust standard errors are obtained.

The main focus of our analyses is to identify potential relationships between species richness and life-satisfaction. We therefore analyzed selected sets of species richness measures. We tested species richness effects in two types of models: a model type with multiple species richness measures (multi-taxon models) and a model type with only a single species richness measure (single-taxon models). All multi- and single-taxon models were estimated with OLS and contained log-transformed species richness variables, and the same set of additional explanatory variables.⁵ The final OLS model results were selected based on AIC values and adjusted r-square values. We present here results from the OLS multi-taxon model with the best model fit (all multi- and single-taxon model results are shown in the Supplementary Tables S6-S13).

To avoid multi-collinearity our multi-taxon models contained only a maximum of three species richness measures at a time: bird species richness, tree species richness and one measure for either mammal or megafauna species richness. In order to further reduce multi-collinearity we calculated the generalized variance inflation factor (GVIF) (Fox and Monette, 1992) and excluded those variables with $GVIF^{1/(2*df)}$ scores >10 before conducting the final analyses (Supplementary Tables S6-S13). Additionally, we excluded explanatory variables that had a pairwise correlation coefficient higher than 0.6 (Dormann et al., 2013). Due to these decisions our final analyses encompass a reduced set of explanatory variables (we excluded population density and heating degree days).

Explanatory variables in the final models representing nature characteristics and climate were landscape and topographic heterogeneity, green and blue space cover, coastline (dummy variable), protected area cover and as a measure of climatic conditions CDD. Socio-economic explanatory variables encompassed income (log net monthly household income), health status, age, the quadratic term of age, gender, residential area (urban or rural), education level, household structure, employment status, information on the person's volunteering behavior and access to local recreation areas. As macro-economic indicators at the level of the NUTS region, we considered unemployment rate and GDP per capita (PPS). To improve model fit, we also tested models with and without the control variables "Eastern Europe" (dummy variable) and "NUTS area size".

All statistical analyses were performed in R Studio Version 1.0.143 (RStudio Team, 2016). Generalized variance inflation factors were calculated with function "vif" ("car" package) (Fox and Weisberg, 2018) and the OLS models were calculated with the "lm" function (package "stats"). For the clustering of standard errors we used the functions "cluster.vcov" from the "multiwayvcov" package (Graham et al., 2016). Ordered logit models with clustered standard errors were calculated with the functions "orm" and "robvcov" ("rms" package) (Harrell Jr., 2019).

4. Results

4.1. Species richness

Bird species richness is positively related to life-satisfaction across

⁵ Landscape heterogeneity, topographic heterogeneity, green space cover, blue space cover, coastline dummy, protected area cover, cooling degree days, recreation access, log net household income, age, age squared, male dummy, urban dummy, education, health, household structure, employment status, volunteering behavior, unemployment rate, GDP per capita (PPS), Eastern Europe dummy and NUTS region area size.

Europe (Fig. 1). This relationship is robust across all multi-taxon and single-taxon model outcomes with p -values below the 5% threshold (Supplementary Tables S6-S13). Mammal-, megafauna- or tree species richness were not significantly related to life-satisfaction (Fig. 1; Supplementary Tables S6-S13).

To assess the strength of the relationship between bird species richness and life-satisfaction we compared the increase in life-satisfaction caused by proportional changes in bird species richness and income (both log-transformed) based on the coefficients (bird coef. = 0.55, 95% CI = 0.05–1.05; income coef. = 0.36, 95% CI = 0.30–0.41) from the econometric model (Fig. 1). An increase in bird species richness by 10% (equivalent to approx. 14 bird species at the median of 136 bird species) is related to an increase in life-satisfaction by a value of 0.052, while an increase in income by 10% (approx. 124 Euro at the median net household income of 1237 Euro) increase life-satisfaction by 0.034. Therefore, an increase in bird species richness by 10% is related to a raise in life-satisfaction approximately 1.53 times more than a similar proportional rise in income (Fig. 2). This effect size does not greatly vary between the models with different species richness specifications since the estimated changes in life-satisfaction based on linear and log-linear bird species richness are very similar (Supplementary Tables S10 and S12). For example, based on the linear coefficients of the multi-taxon models (Supplementary Table S10) a 10% increase in bird species richness (14 species) would increase life-satisfaction by a value of approx. 0.07 (similar to the log-linear specification). However, please note that the confident intervals for the coefficient estimates are considerably higher for bird species richness than for income (Fig. 1) and therefore the true effect of bird species richness might be smaller, or greater.

In addition, we predicted how life-satisfaction values might increase along the range of bird species richness values within each country (Fig. 3). Based on the OLS model results presented here (Fig. 1) we first predicted life-satisfaction values for each NUTS region and afterwards calculated average values for each European country. For example, in Spain, the country with the largest range of bird species richness, life-satisfaction is predicted to increase by 0.45, if the bird species richness within a region would change from lowest national value to the highest value, provided a person's socio-economic status and other factors remain the same (Fig. 3). Under the same scenario, the average estimated change in life-satisfaction within all 26 European countries has a value of 0.12 (SD = 0.11).

To validate our OLS results, we tested whether the within-region (NUTS region) variance of our species richness variables was a major factor in explaining the overall variation of species richness across Europe (between-region variance). The results indicate that a much larger part of the total variance of bird species richness across Europe is driven by the between-region (61.4%) variance than within-region variance (38.6%) (Supplementary Table S5). We can therefore assume that the within-region variance of bird species richness has little influence on our overall results.

4.2. Other nature characteristics and climate

We also tested the influence of other nature and climate characteristics on life-satisfaction and find a positive relationship between an individual's access to recreational areas and life-satisfaction (Fig. 1, Supplementary Tables S6-S13). Across all the OLS models we find that life-satisfaction increased when people had easy or very easy access to public green spaces and recreational areas. Based on the presented OLS model (Fig. 1) the life-satisfaction scores might improve by 0.32 (95% CI = 0.02–0.62) when a person had easier access to recreational areas compared to access with great difficulty. When the access was very easy the life-satisfaction scores increased by 0.54 (95% CI = 0.24–0.83). For all other characteristics we find no significant effects on life-satisfaction (Fig. 1, Supplementary Tables S6-S13). Neither landscape heterogeneity, topographic heterogeneity, protected area cover nor climate have a

significant association with life-satisfaction.

5. Discussion

This is the first continental study which explores the non-material associations between species diversity and life-satisfaction, while accounting for socio-economic factors and other nature characteristics. Our results show that bird species richness is related to life-satisfaction across Europe, and that this association may be comparable in magnitude to that of income. Due to the large confidence intervals, however, the true effect size of bird species richness might be lower, or higher than reported here. In addition, we find no significant relationships with life-satisfaction for mammal-, megafauna- or tree species richness as well as for other nature characteristics and climate.

5.1. Bird species richness and life-satisfaction

With regard to bird species richness, our results correspond to previous findings from local level studies on species richness and human well-being. For instance, visitors to urban parks with higher bird species richness exhibit better psychological well-being scores than those visiting parks with lower species richness (Fuller et al., 2007). In an urban neighborhood bird species richness was found to influence personal and neighborhood well-being (Luck et al., 2011), while on the national level, subjective health was positively related to bird species richness (Wheeler et al., 2015). Furthermore, listening to bird songs can reduce psychological stress (Alvarsson et al., 2010; Medvedev et al., 2015) and has a positive influence on perceived attention restoration and stress reduction (Ratcliffe et al., 2016; Ratcliffe et al., 2013).

This relationship between bird species richness and life-satisfaction might change depending on the spatial units used in the analyses. Our main results are calculated with bird species richness data collected at the level of 50 × 50 km grid cells and averaged within the NUTS regions. While it would be interesting to test our research question with finer spatial resolution data (e.g. 10x10km grid), no such data on species richness is consistently available across Europe. With regard to the effect size, our findings show that larger the effect of bird species richness on life-satisfaction may be of similar magnitude to that of income. Access to green space and recreational areas had a stronger overall effect on life-satisfaction with higher life-satisfaction scores when accessibility was "easy" or "very easy" (Fig. 1), but these two variables are difficult to compare as one is a continuous and the other a categorical variable. However, these results still suggest that bird species richness, like income, access to green space or other factors, is important for life-satisfaction at a continental level (e.g. Diener and Biswas-Diener, 2002; Dolan et al., 2008; Ma et al., 2019). An interesting future research avenue could be to test the effect of changes in income over time on life satisfaction in comparison to changes in species diversity and access to green space.

These results need to be interpreted with caution, however, as our results do not reveal causal relationships but correlations. Due to the spatial level of the analyses, it is unknown at which spatial scale people experience bird species richness and also the pathways of such experiences are hypothetical (see 5.2 Suggested mechanisms). Possible strategies to prove a causal relationship between bird species richness and life satisfaction are to carry out longitudinal studies (e.g. Alcock et al., 2014; White et al., 2013a) or to use experimental techniques that include mediators (e.g. Marselle et al., 2016). Unfortunately, we were not able to analyze time series data or conduct experiments, as currently only cross-sectional (one point or period in time) data is available for bird species richness in Europe and experiments are not feasible on such a spatial level. Nonetheless, the magnitude of the relationship between bird species richness and life-satisfaction and the quantitative comparison with income indicate potentially strong and socially relevant relationships.

5.2. Suggested mechanisms

Possible mechanisms for the positive relationship between bird species richness and well-being, in this case measured as life-satisfaction, are not well understood (Aerts et al., 2018; Hartig et al., 2011; Marselle et al., 2019). We argue that at the large spatial scale of this study two types of possible, and non-exclusive, pathways exist that may explain how bird species richness affects life-satisfaction: the effect of the direct visual and auditory experience of birds, and an effect of experiencing landscapes with features which promote both bird species richness and human well-being, making bird richness a proxy indicator of the true landscape drivers. With regard to the first pathway, seeing and observing birds and their behavior in gardens (Cox and Gaston, 2015) or in wild nature (MacKerron and Mourato, 2013) can promote positive emotions and increase well-being. A recent study could show that high bird species richness increases the positive emotional response of visitors to urban green space (Cameron et al., 2020). In an experimental online survey, participants who watched videos with high bird species richness report less anxiety (Wolf et al., 2017). One possible explanation for this positive effect might be that many birds are aesthetically appealing to humans, and relatively easy to observe compared to many other taxa. People value birds for their physical beauty, interesting behavior and pleasing songs (Belaire et al., 2015; Hedblom et al., 2014; Medvedev et al., 2015). Birds are hence one of the most “loved” biological elements by people at their favorite outdoor places (Schebella et al., 2017). In addition, songbirds and higher richness of birds are preferred over non-singing birds or higher numbers of the same bird species (Cox and Gaston, 2015). Species that are less favored tend to be pigeons, seagulls or crows (e.g. Bjerke and Østdahl, 2004), however, these unpopular species constitute only a very small proportion of overall bird species richness.

Alternatively, high bird species richness may serve as an indicator for regional and local landscape properties which themselves promote life satisfaction. At the regional scale, landscapes with high landscape diversity tend to have high bird species richness (e.g. Gil-Tena et al., 2007), and landscape elements that also have high aesthetic or recreational value are also associated with bird diversity (Oteros-rozas et al., 2018; Velarde et al., 2007). Therefore, bird species richness might be a better indicator of the recreational quality of natural landscapes than the other nature characteristics (e.g. landscape heterogeneity, protected area cover) used in this study (see section 5.4). Correspondingly, bird species richness has been used as an indicator for environmental quality in health studies (Wheeler et al., 2015) or has been included in composite measures of landscape diversity, as in the Swiss Biodiversity Monitoring program (Weber et al., 2004). Locally, high bird species richness is related to greater availability of natural space in urban areas (Loss et al., 2009), including high vegetation cover and the existence of water bodies (Beninde et al., 2015), nature characteristics which also positively influence human health and well-being (Cox et al., 2017; Luck et al., 2011; Völker and Kistemann, 2011).

Suggested mediators that link bird species richness to life satisfaction either directly or as a proxy for beneficial landscape properties are attention restoration and stress reduction. These two mediators correspond to two psychological theories, the Attention Restoration (Kaplan, 1995) and the Stress Reduction Theory (Ulrich, 1991). Both theories are well established in the nature-human health framework, for instance, as mechanisms that link positive effects of green space to human health (Hartig et al., 2014; Markevych et al., 2017). Correspondingly, experiencing birds might restore attention fatigue (Dallimer et al., 2012; Fuller et al., 2007; Marselle et al., 2016) or reduce stress (Cox et al., 2017; Wolf et al., 2017). Certain landscape properties such as habitat diversity might increase well-being via the same two mediators (Carrus et al., 2015; Fuller et al., 2007; Hipp et al., 2016). Recently, it has been suggested that positive emotions might be a third potential mediator linking species diversity and well-being (Irvine et al., 2019), offering an additional explanation for the observed correlation.

It would be interesting to gain a better understanding of the mechanisms that link species diversity and life-satisfaction. However, the lack of appropriate variables (e.g. frequency and duration of bird experiences) did not allow us to investigate the significance of the possible pathways here. Further research is therefore necessary to examine the pathways and mediators, especially across larger spatial scales (e.g. Europe). We were also not able to test whether bird abundances can be linked to life-satisfaction as regional and local bird abundance data is not consistently available across all European countries (but see British or German breeding bird atlases). Future research should also investigate the potential effect of bird traits since conspicuousness and detectability due to size, plumage, song or behavior, as well as perceived beauty may have a strong influence on life-satisfaction (e.g. Cox et al., 2017).

5.3. No effects of mammals and trees

We did not find any association between our mammal and megafauna richness variables and life-satisfaction (Supplementary Tables S6-S13) despite the fact that mammals and especially large charismatic mammals, i.e. megafauna, can trigger positive emotional responses in humans (Curtin, 2009; Methorst et al., 2020) and foster connection to nature (Bruni et al., 2008; Cousins et al., 2009). The results for the mammal and megafauna species richness variables can be influenced by the possibility that people, especially urban residents, might not regularly encounter mammals because many mammalian species are evasive and tend to avoid places with high human population density and mainly occur in rural or less populated areas (Basille et al., 2013; Gaynor et al., 2018; Sol et al., 2013), while small mammals and bats are often difficult to detect even when present. Many birds, on the other hand, can be perceived, even subconsciously, by people due to their songs, even if they might not be visible in the vegetation, and are often very active and detectable in human vicinities (e.g. bird feeding). In addition, people tend to have negative attitudes or emotions towards many mammals as they consider several species dangerous or a nuisance (e.g. Methorst et al., 2020; Røskoft et al., 2003; Soulsbury and White, 2015), so effects could indeed be neutral or even negative for some mammal species.

With regards to tree species richness, we also did not find a significant effect on life-satisfaction, even though higher levels of tree diversity can positively influence mental well-being when watching videos in an online experiment (e.g. Wolf et al., 2017). However, when people are outdoors they might be affected rather by local vegetation cover and structure, and overall plant species richness (Dallimer et al., 2012; Hoyle et al., 2017; Lindemann-Matthies and Matthies, 2018; Luck et al., 2011) or by street tree abundance in their neighborhood (Taylor et al., 2015) than by regional patterns of tree species richness. Unfortunately, data for measures of total plant diversity were not available at the large spatial scale of our study.

5.4. Effects of access to parks, other nature characteristics and climate variables

We find that life-satisfaction is higher when people reported easy or very easy access to public green spaces and recreational areas, which confirms findings in other studies regarding life-satisfaction and other well-being measures (Cleary et al., 2019; Kabisch, 2019; Krekel et al., 2016; Ma et al., 2019). This result is not surprising considering that people are more likely to visit parks and natural areas, and thus obtain well-being benefits when green space is located closer to home (Coombes et al., 2010; Dallimer et al., 2014; Ekkel and de Vries, 2017; Schipperijn et al., 2010).

For the other nature characteristics, we were unable to confirm results of earlier studies that show an association of the amount of area covered by green or blue space and human well-being (de Vries et al., 2016; Gascon et al., 2015; Maas et al., 2006; White et al., 2017). We also did not find a significant relationship between protected area cover or

landscape heterogeneity and life-satisfaction, despite evidence that shows that such nature characteristics influence human well-being (Wheeler et al., 2015; Wyles et al., 2019).

A possible explanation for this result may be that our measures of nature characteristics might not reflect landscape quality at the large scale of this study, or how people experience nature and specific nature characteristics. For example, our measure of landscape heterogeneity includes various categories for artificial surfaces that contribute to heterogeneity but may not reflect landscape quality for humans. Instead, bird species richness may be a better indicator of local landscape characteristics important also to the well-being of humans (see above section 5.2). Furthermore, positive effects of nature characteristics such as landscape heterogeneity on human well-being are often found on finer spatial scales (e.g. Carrus et al., 2015; Rantakokko et al., 2017), e.g. within urban areas. However, such fine-grained data in combination with people's socio-economic data are not available for Europe.

Earlier studies found that climate, as represented by various temperature and precipitation variables, can influence life-satisfaction and happiness (Murray et al., 2013; Rehdanz and Maddison, 2005). Studies testing degree days in order to compare their results to ours are few. Recently, however, a global study also tested cooling and heating degree days and found a significant negative relationship between cooling degree days and high life-satisfaction scores and no relationship for heating degree days (Chapman et al., 2019). Similarly, another global study could show that cooling degree months are negatively associated with life-satisfaction (Maddison and Rehdanz, 2011). Further research is necessary in order to better understand why different measures for climate have dissimilar effects on life-satisfaction on a continental level.

6. Conclusions

Here we demonstrate that bird species richness is positively related to life-satisfaction across Europe, with a comparable effect to income. This result highlights the potential non-material link between species diversity and human well-being. Within the context of the IPBES framework (Díaz et al., 2018), this means that bird species richness may also provide non-material NCP to human well-being on a continental level. This information may turn out to be crucial for evidence-based policy decisions regarding environmental management (Adams and Morse, 2019) and nature-based solutions to improve human health and well-being (Cariñanos et al., 2017; Marando et al., 2016; Vujcic et al., 2017). Future research needs to further investigate and confirm the causal links of this observed relationship and explore the mechanisms involved including positive emotions, attention restoration and stress reduction (Aerts et al., 2018; Irvine et al., 2019; Marselle, 2019) or the possibility that, on a large spatial scale, bird species richness might simply be a proxy for beneficial landscape properties (e.g. landscape aesthetics, landscape diversity) or environmental quality. Even if this is the case it may prove that managing for bird diversity is a win-win strategy, with both humans and birds benefitting from management actions that promote a high diversity of natural landscape features.

The recent IPBES global and regional assessments warned that the future provision of NCP may be threatened due to increasing biodiversity loss, mainly caused by land-use change and exploitation (IPBES, 2019; 2018). In the context of our study, current declines in bird species richness and abundances in Europe and North America (e.g. Bowler et al., 2019; Rosenberg et al., 2019) could potentially also result in lower levels of human well-being. So far, the protection of birds and bird habitat has been conducted as a means of protecting bird diversity (European Union, 2010). However, this study may show that the conservation of birds and the landscapes and habitats that support them would be a very worthwhile investment in human well-being. Political and societal decision making should encourage the maintenance and creation of natural areas that support high bird diversity, thus fostering synergies between biodiversity conservation and promotion of human well-being.

Author contributions

J.M., K.R. and K.B.-G. designed the study. J.M. carried out data compilation and analysis. K.R., K.B.-G. and T.M. contributed to the data analysis. J.M. wrote the initial draft of the manuscript. All authors contributed substantially to the writing of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary information

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