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RESEARCH ARTICLE

# Species richness and evenness of European bird communities show differentiated responses to measures of productivity

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## Abstract

1. Understanding patterns of species diversity is crucial for ecological research and conservation, and this understanding may be improved by studying patterns in the two components of species diversity, species richness and evenness of abundance of species. Variation in species richness and evenness has previously been linked to variation in total abundance of communities as well as productivity gradients. Exploring both components of species diversity is essential because these components could be unrelated or driven by different mechanisms.
2. The aim of this study was to investigate the relationship between species richness and evenness in European bird communities along an extensive latitudinal gradient. We examined their relationships with latitude and Net Primary Productivity, which determines energy and matter availability for heterotrophs, as well as their responses to territory densities (i.e. the number of territories per area) and community biomass (i.e. the bird biomass per area).
3. We applied a multivariate Poisson log-normal distribution to unique long-term, high-quality time-series data, allowing us to estimate species richness of the community as well as the variance of this distribution, which acts as an inverse measure of evenness.
4. Evenness in the distribution of abundance of species in the community was independent of species richness. Species richness increased with increasing community biomass, as well as with increasing density. Since both measures of abundance were explained by NPP, species richness was partially explained by energy-diversity theory (i.e. the more energy, the more species sustained by the ecosystem). However, species richness did not increase linearly with NPP but rather showed a unimodal relationship. Evenness was not explained either by productivity nor by any of the aspects of community abundance.
5. This study highlights the importance of considering both richness and evenness to gain a better understanding of variation in species diversity. We encourage the study of both components of species diversity in future studies, as well as use of simulation studies to verify observed patterns between richness and evenness.

KEYWORDS
abundance distributions, community dynamics, evenness, multi-species, productivity, spatiotemporal, species richness, time-series

## 1 | INTRODUCTION

Species diversity is of great importance for many aspects of ecosystem structure and function (Hooper et al., 2005; McCann & Gellner, 2020). To comprehend the factors that sustain and shape it, we must consider the multitude of mechanisms influencing species diversity (Palmer, 1994; Terborgh, 2015). These mechanisms encompass historical events (Mittelbach et al., 2007; Ricklefs, 2004; Svenning & Skov, 2007), climate and habitat heterogeneity (Currie et al., 2004; Kerr & Packer, 1997; Stein et al., 2014), as well as bottom-up and top-down effects stemming from species interactions and trophic complexity (MacArthur, 1984; Paine, 1966). The interplay of these mechanisms (Engel et al., 2022; Pontarp et al., 2019; Ricklefs, 1987) makes it challenging to predict how environmental changes will affect community composition and ecosystem processes. Furthermore, the concept of species diversity comprises two components: species richness (the number of species in a community) and evenness (the degree of variance among species abundances—i.e. evenness is highest when this variance is low; Magurran, 2013). While these two components were initially assumed to be strongly positively related (DeBenedictis, 1973; Hill, 1973; May, 1975), species richness alone has often been studied along ecological gradients. However, subsequent research has revealed positive, neutral, as well as negative relationships between richness and evenness (e.g. Sæther et al., 2013; Soininen et al., 2012; Stirling & Wilsey, 2001; Sugihara, 1980; Zhang et al., 2012). This indicates that richness and evenness may be governed by distinct sets of mechanisms, and thus, there have been many calls for treating them as separate measures of species diversity (e.g. Magurran, 1988; Weiher & Keddy, 1999; Whittaker, 1965).

Species diversity exhibits distinct latitudinal patterns (Hillebrand, 2004; Lyons & Willig, 2002; Rohde, 1992). Net primary productivity (NPP), strongly correlated with latitude, plays a pivotal role as initial source of energy and matter for heterotrophs, making it a vital variable for understanding species diversity. Notably, productivity emerged as the best predictor of species richness in a comparative study of spatial richness gradients including non-experimental studies of both plants and animals (Field et al., 2009). Several hypotheses attempt to explain the relationship between species diversity and productivity. One hypothesis suggests that species richness in a given area should increase with primary productivity (Currie, 1991; Hutchinson, 1959; Lawton, 1990; Rosenzweig, 1995; Wright, 1983). This relationship hinges on the assumption that areas with higher productivity can support more individuals, thus fostering a greater species richness with viable population sizes (Currie et al., 2004; Rosenzweig & Abramsky, 1993; Srivastava & Lawton, 1998). Numerous studies have observed a linear increase in species richness with increasing productivity (e.g. Gaston, 2000; Mittelbach et al., 2001; Turner et al., 1988). McNaughton et al. (1989) found the biomass of terrestrial primary consumers to be a function of NPP raised to the power of approximately 1.5. Such findings indicate that, the more energy that enters the system, the more biomass is available for partitioning among individuals of different species. If species richness is influenced by the number of individuals in an area, a positive correlation should also exist between density (i.e. the number of territories per area) and species richness in the community (Currie et al., 2004). This pattern has been well-documented in bird communities (see e.g. Currie et al., 2004; Evans et al., 2008; Hurlbert, 2004; Meehan et al., 2004; Mönkkönen et al., 2006).

Another mechanism that can account for species richness in productive areas is the niche-specialization hypothesis (see e.g. Schoener, 1976; Srivastava & Lawton, 1998). According to this hypothesis, more productive areas should host a greater species richness by allowing for a broader range of niches and/or by permitting species to become more specialized. Habitat complexity can additionally affect niche specialization and thus the observed relationship between diversity and productivity. More complex habitats (such as forests) have been found to sustain higher species richness compared to simpler habitats (such as grasslands and mashes) at equivalent levels of productivity (Ricklefs & Whiles, 2007).

Numerous studies have reported an initial increase followed by a decrease in species richness with increasing productivity, resulting in a 'hump-shaped' relationship (see e.g. Fraser et al., 2015; Mittelbach et al., 2001; Rosenzweig, 1995). This suggests the presence of mechanisms limiting species richness also in high productive areas. One proposed explanation posits that richness might be constrained by resource competition at low productivity levels, increase as productivity rises, and then decline in highly productive areas where superior competitors outcompete other species (Al-Mufti et al., 1977; Grime, 1973; Rosenzweig & Abramsky, 1993). Other mechanisms have also been explored. For example, in their study of pond communities, Chase and Leibold (2002) found that the richness-productivity pattern was scale-dependent; transitioning from a hump-shaped to a positive relationship with an increasing study area. Conversely, scale-independent patterns have been observed in plant communities (Lisner et al., 2021) and in birds (Evans et al., 2008). Colwell and Hurtt (1994) argued that the unimodal relationship may arise from randomly generated species ranges. For instance, a central maximum richness, such as in mid-latitude areas, could result from increased overlap of bounded species ranges in the middle of the domain (Colwell & Hurtt, 1994; Colwell & Lees, 2000). Nevertheless, a comparative study of research indicates that environmental conditions, rather than the mid-domain effect, best predict geographical variation in species richness (Currie & Kerr, 2008).

Evenness, the degree of variance among species abundances, also plays a crucial role in shaping species diversity. A general pattern that has been suggested is that there could be a tendency for evenness to increase with productivity (McGill et al., 2007). According to the pioneering studies of MacArthur and collaborators in the 1960s (summarized in MacArthur, 1972; see also Loreau, 2010) we would expect tighter species packing and greater evenness with increasing primary productivity, simply because more resources are available, allowing more competing species to coexist within the same area. Evidence for such bottom-up regulation of evenness has been challenging to obtain (Terborgh, 2015), and studies investigating this relationship in birds have produced contradictory conclusions (Harrower et al., 2017; Hurlbert, 2004).

In summary, the relationship between the two components of species diversity—richness and evenness—is complex, and multiple mechanisms can influence their patterns along ecological gradients. While various hypotheses attempt to explain these patterns, none has received unequivocal support (He & Legendre, 2002). The complexity of this relationship is further compounded by the inherent difficulty in estimating true species richness and evenness. Analyses of community composition are grounded in samples of individuals drawn from larger ecosystems. Consequently, any inferences drawn must be sensitive to the effects of sampling procedures (Dornelas et al., 2013). Studies covering ecological gradients inevitably implies community samples of limited size, and not accounting for biases (e.g. observed species richness underestimates true species richness) and sampling variation may have a negative impact on our ability to detect patterns. However, one promising approach to address these challenges is by leveraging parametric species abundance distributions (May, 1975; Sæther et al., 2013) which can account for these complexities. One notable advantage of assuming an underlying species abundance distribution lies in the ability to elucidate the influence of sampling on observed species abundances, predicated on realistic sampling assumptions.

In this study, we harness the statistical properties of the zero-truncated Poisson log-normal species abundance distribution, enabling us to simultaneously estimate the expected species richness in the community as well as the evenness of the community (Sæther et al., 2013). This species abundance distribution assumes Poisson distributed samples from a lognormal distribution of abundances among species within the community. The variance parameter of the lognormal distribution provides an estimate of the evenness component of species diversity, with a small variance indicating a more even community (Grøtan et al., 2012; Sæther et al., 2013). The zero-truncated distribution accounts for species present in the community but absent in samples, thereby providing estimates of species richness and evenness of the community rather than solely for the sample. We first examine the relationship between the two components of species diversity, and then relate the variation in each of them to latitudinal and productivity gradients and examine how they differ across different habitat types. Our goal is to examine key variables for predicting spatial variation in species diversity of birds over large geographical areas.

## 2 | METHODS

### 2.1 | Data

#### 2.1.1 | Territory mapping data

The dataset used here is a collection of high-quality censuses of bird populations across Europe based on mapping of territories in fixed study plots, following the method originally developed by Enemar (1959). This standardized method involves multiple visits during the breeding season where every pair of each species is mapped. The method also involves a long-term commitment to monitor the study plot for multiple years. The initial data set inspected for suitability for our analysis consisted of $n=1411$ plots. After data selection and model application (described in detail later), the dataset encompassed $n=376$ plots (open habitat: $n=289$, forest habitat: $n=87$) and consisted of community time-series of 13–117 species (Mean: 46 species) monitored for 6–50 years (Mean: 12 years), censused between 1950 and 2018. The data sources for this study are as follows: 276 of the plots come from the British Trust for Ornithology's (BTO) Common Bird Census (CBC) and the BTO/Joint Nature Conservation Committee/Royal Society for the Protection of Birds, Breeding Bird Survey (BBS; Freeman et al., 2007; Marchant, 1990). Two additional plots from the UK were obtained from Williamson (1975) and Gaston and Blackburn (2008). Seventy-eight plots from Germany were provided by Bowler and Schwarz (pers. comm.), see Schwarz and Flade (2000) and Kamp et al. (2021). Two plots from Estonia were provided by Leivits (pers. comm.). Seven plots from Poland were obtained from Tomiałojć and Wesołowski (1996) and Wesołowski et al. (2002). In total, six plots from Sweden were obtained from Enemar et al. (2004), Svensson (2006, 2009). Two plots from Finland were obtained from Palmgren (1987) and Lehikoinen et al. (2016), and three plots from Norway were included (own data, as well as Moksnes (1978) and Hogstad (1993)). See Appendix S1: Figure S1, and Figure S2 and Appendix S7: Table S1 for more details.

#### 2.1.2 | Measures of community abundance

Here, we used community biomass as well as density as two separate measures of community abundance. In classical Lotka-Volterra competition equations, species are thought to influence each other through a set of competition coefficients (Lotka, 1925; Volterra, 1926). On the level of the community, an analogous assumption that can be made is that all species contribute to a combined 'competition pressure', affecting the species in the community (see e.g. Ovaskainen et al., 2017; Sandal et al., 2022). The measure of density takes into account the number of pairs a given area can sustain, and the community biomass metric additionally takes into account that the 'competition pressure' exerted by a large individual might be greater than that of a small one. To obtain a measure of community biomass per area, we utilized body mass data from Dunning Jr (2007). Whenever possible, we chose the measure for male birds (because territory mapping is based on identifying territorial males) from Eurasia. For each species in each plot and year, we first multiplied the counts of a given species by its species-specific body mass. Subsequently, we summed the biomass of all the species in a given plot and year and divided these values by area. In a final step, we averaged the area-corrected yearly community biomass metrics for each plot, thus yielding one community biomass metric per plot.

To obtain a measure of density, we summed the counts of all species in each plot and year and divided this value by plot area. Subsequently, we take the average of these area-corrected yearly densities within each plot, to obtain one value per plot. As mentioned, the counts in territory mapping refer to territorial males, and thus the values of density reflect the number of territories per area.

### 2.1.3 | NPP and GPP

To obtain an estimate of productivity for each plot, we accessed data for annual net primary production (NPP) from https://lpdaac.usgs.gov/ (MOD17A3HGF Version 6 product; 500 m pixel resolution) using the R-package 'MODIS' (Mattiuzzi & Detsch, 2020) in October 2020. We extracted the mean value of NPP across the years available (2002–2016; i.e. the average of the mean annual values of NPP for each plot) from a 1 × 1 km grid around the plot coordinates (alternatively increasing the buffer by 500 m until the first non-NA value could be determined). We additionally investigated whether gross primary productivity (GPP) during the breading season (April–July) was a better predictor than NPP. For this, we additionally accessed the MOD17A2H Version 6 product (cumulative 8-day composite values, 500 m pixel resolution) in July 2023 (Running et al., 2015). We extracted values of GPP in the same way as described above. NPP and seasonal GPP were strongly correlated, see Appendix S5: Figure S3.

### 2.1.4 | Land cover data

We accessed the European Space Agency's Climate Change Initiative (ESA CCI) annual land-cover maps from 1992 to 2015 with 300 m resolution (https://www.esa-landcover-cci.org/) in October 2020 (ESA, 2017). These maps categorize the Earth's surface into 37 land cover classes (LC), following the United Nations' Land Cover Classification System (UN-LCCS; Di Gregorio, 2005). A continuation of these maps for the years 2016–2018 was accessed through the Copernicus Climate Change Service (C3S) Climate Data Store (CDS; https://cds.climate.copernicus.eu/) in October 2020. Note that the maps from CDS make use of only 22 of the UN-LCCS classes.

We extracted each year's dominant land-cover class for each plot with a buffer of 300 m around the coordinates. If LC changed during the observation period, we selected the LC with the most observations for a given plot ($n = 6$). For some plots, not all of the observations were covered by the LC- time-series, and in these cases, we also selected the LC with the most observations ($n = 165$, Mean percentage of years covered by the LC–time-series in these cases was 52.36 (SD = 24.07)). If all observations were made before the LC time-series started ($n = 96$), we chose the first LC registered (i.e. the LC in year 1992) for that plot. For further analysis, we utilized this information to divide the plots into two rougher categories: 'open' and 'forest', reflecting simpler and more complex habitat types, respectively (see Appendix S1: Table S1 for more details).

### 2.1.5 | Data selection

In this study, we excluded plots with a total of <10 species and/or if the mean average number of counts per year was <30, as the reliability of parameter estimates in such plots may be compromised. Based on the extracted land-cover information, we excluded plots belonging to urban areas. Based on the LC information for each plot, we combined observations from neighbouring plots within a radius of 2 km into clusters if the LC was the same. If the observed time-series for these plots overlapped, we summed the count and the area values (otherwise they were treated as separate plots). The final dataset contained two such clusters, combining information from two plots each.

## 2.2 | Statistical framework

The Poisson log-normal distribution (PLND) offers a number of statistical properties that are of importance for ecological inference. For instance, the variance of this distribution provides information on community structure: A small variance indicates that most species are equally abundant, while a large variance points to a few species being more than average dominant in the community. Thus, the variance of the PLND acts as an inverse measure of evenness (Sæther et al., 2013). In addition, the true underlying species richness can be estimated from the probability density function of the distribution (Grøtan & Engen, 2022). The PLND, first described by Grundy (1951), has been widely used for ecological study since its first application by Bulmer (1974) (see e.g. Bulmer, 1974; Connolly & Dornelas, 2011; Grøtan et al., 2012; Sæther et al., 2013). Here, we extend this statistical framework by applying a multivariate PLND to each location of our time-series data, allowing us to utilize the entire community data simultaneously in our inferences. Such multivariate PLND have recently been suggested to be a versatile tool for ecological studies (Chiquet et al., 2021).

We assume the true underlying abundances, $N_1, \ldots, N_i$, of the $i$ different species in a given plot and year to be realizations from a log-normal distribution with expectation $m$ and variance $\sigma^2$. The observed abundances for each species in turn are considered to be a draw from a Poisson distribution with the true abundance $N_i$ being the expectation (and variance) ($\lambda$). Thus, the vector of abundances of a community is described by the Poisson lognormal distribution, $P_{\mathrm{PLN}}(\mu, \sigma^2)$, with mean $\mu = (m + \ln v)$, where $v$ is the sampling intensity, and variance $\sigma^2$. Note that sampling intensity is constant for a given location in our data.

Two samples from a community taken with time difference $t$ can each be described by such a PLND, and their joint distribution follow a bivariate PLND (Engen, Grøtan, et al., 2011). This joint distribution is described by a mean (μ) and variance ($\sigma^2$) parameter for the marginal distributions of each community sample, as well as a correlation ($\rho$) between the two ($\mu_1, \sigma_1^2, \mu_2, \sigma_2^2, \rho_t$). Previous studies have fitted the bivariate PLND distribution to all pairs of samples to study community similarity (e.g. Engen, Grøtan, et al., 2011; Grøtan et al., 2012, 2014) and to decompose the variance of the lognormal species abundance distribution (e.g. Engen et al., 2002; Engen, Aagaard, et al., 2011). However, such an approach treats each pair of samples as independent, and species identity is not shared across pairwise samples.

Here, we instead simultaneously utilize all samples in time of a given community to directly estimate the community variance, $\sigma^2$, the correlation function of relative species abundances at different time-lags as well as the community richness, $S$. Thus, instead of averaging values obtained for a community for each year, this approach allows us to take into account autocorrelation in relative species abundances and species identity across all samples in time. Such an approach can stabilize estimates because information is drawn from multiple data-points in time.

### 2.2.1 | Model

Our model is essentially an implementation of the theoretical framework developed by (Engen, 2007; Engen et al., 2002; Engen, Grøtan, et al., 2011; Engen & Lande, 1996; Lande et al., 2003), who found that a community in which the species are governed by a Gompertz' type of density regulation produces a log-normal species abundance distribution, even when allowing growth rates to differ among species. Although the log-normal distribution can also arise from neutral dynamics (e.g. Bell, 2001; Hubbell, 2011), density regulation is known to be important in natural populations of a wide range of taxa including birds (Brook & Bradshaw, 2006; Sandal et al., 2022), supporting the framework. Based on this theoretical foundation, we build a model that allows us to estimate the parameters needed for our inferences in the best possible way.

We let the vector of the log abundances of species $i$ across all years, $\log(\lambda_i)$, at a given location be modelled as a realization of a multivariate normal distribution defined by the vector $\boldsymbol{\mu}$ of yearly mean log abundances (indexed by $t$ below), as well as by a variance–covariance matrix (Σ):

$$\log(\lambda_i) \sim \mathrm{MVN}(\boldsymbol{\mu}, \Sigma). \tag{1}$$

The yearly mean log abundances $\mu_t$ are dependent upon a community mean abundace $\overline{\mu}$ across years, a trend in $\boldsymbol{\mu}$; $\partial$ (defined through $\eta_t$ as described below) and variance $\sigma_c^2$:

$$\mu_t \sim \mathrm{N}\left(\overline{\mu} + \eta_t, \sigma_c^2\right). \tag{2}$$

Potential trends in $\boldsymbol{\mu}$ are accounted for by the parameter

$$\eta_t = \dot{\eta}_t - \overline{\dot{\boldsymbol{\eta}}}, \tag{3}$$

where $\dot{\eta}_t = \partial \times t$ ($\partial$ being the trend in $\boldsymbol{\mu}$). If there is no evidence for such a trend, $\eta_t$ will simply become 0.

Ecologically speaking, $\overline{\mu}$ is related to the general habitat quality in which the community exists. For instance, a generally favourable habitat may allow for a larger community mean abundance. Trends in $\boldsymbol{\mu}$ may arise for example from long-term changes in climatic conditions. $\sigma_c^2$ corresponds to year-effects due to common environmental noise such as a severe winter, pollution or other events that affect all species equally, as well as competition effects that act equally on all species, such as competition for space and nutrients (Lande et al., 2003).

The community is further defined by the variance–covariance matrix (Σ), with the community variance $\sigma^2$ as its diagonal elements, and $\sigma^2 \times \rho_t$, where $\rho_t$ is the correlation at time difference $t$, as its off-diagonal elements. In log-linear time-series models with intraspecific density-dependence, the function of the autocorrelation in the time-series of a population is commonly described by $e^{-\gamma t}$ (e.g. Royama, 1992; Turchin & Taylor, 1992), where $t$ is the distance in time between the two samples and $\gamma$ is a scaling parameter.

Interspecific variation among species in expected log-abundance may cause correlations to approach $\rho_\infty$ instead of 0 even for large time differences (Engen, Grøtan, et al., 2011). Thus, the correlation $\rho_t$ (between two samples of the community) with time-lag $t$ can be defined as:

$$\rho_t = \left(\rho_0 - \rho_\infty\right)\rho^{-\gamma t} + \rho_\infty, \tag{4}$$

where $\rho_0$ is the intercept (i.e. the expected correlation at $t$=0. Note that $\rho_0$ can be lower than 1 due to overdispersion), $\rho_\infty$ is the correlation towards which the community tends in the long run, and $\gamma$, as before, is a scaling parameter.

A well-known pattern in community ecology is that increasing sample size (sampling intensity, sampling area, repeated sampling in time) increases the number of observed species. The least abundant species may be observed only in few, and some species in none, of the samples. The number of unobserved species can be estimated by formulating the PLND as a zero-truncated distribution (e.g. Grøtan et al., 2022; Sæther et al., 2013). While the two-dimensional integral required to calculate the probability of a species not being included in any of the two smaples can be calculated in a bivariate PLND, performing the multi-dimensional integral required in a multivariate model is unfeasible. Here, following (e.g. Kéry & Royle, 2020; Royle et al., 2007) we instead augment the data with multiple 'species' with 0 observations across all years and use a zero-inflated model (see e.g. Kéry & Royle, 2020; Royle et al., 2007; Zuur et al., 2009) to facilitate the process of estimating the true species richness in the community.

To account for zero-inflation, we model the counts (including the augmented data), $C$, for a given species ($i$) in a given year ($t$) as

$$C_{i,t} \sim \mathrm{Poisson}\left(a_i \times \lambda_{i,t}\right), \tag{5}$$

That is we let $C_{i,t}$ be a realization of the Poisson distribution with expectation $\lambda_{i,t}$ (see Equation 1). $a_i$ is a realization from a Bernouilli distribution with a probability $\pi$ of being 1.

The estimated true species richness in the community could be obtained from the observed species richness as $S = S_{\text{obs}} \times (1 - \pi)$. However, our implementation of the model (see section below) allows for estimation of $S$ as the sum of the discrete latent variables $a_i$.

### 2.2.2 | Implementation

We implement our model (Equations 1–5) using the R-package 'nimble' (de Valpine et al., 2020), using MCMC computation to find the joint posterior distribution of the parameters $(\overline{\mu}, \partial, \sigma_c^2, \sigma^2, \rho_0, \rho_\infty, \gamma, \pi)$. See Appendix S2 for a description of the priors used. We sampled two MCMC chains, each with 3.200.000 iterations, discarded the first 200.000 iterations as burn-in, and thinned the remaining by thin = 50, yielding 60,000 MCMC samples per chain, that is 120,000 samples in total.

We evaluated MCMC convergence by visually checking posterior trace plots, as well as by examining the potential scale reduction factors ($\hat{R}$) of the model parameters (see Appendix S3: Figure S1), using the R-package 'coda' (Gelman & Rubin, 1992; Plummer et al., 2006). Plots for which the average $\hat{R}$ of the estimated parameters was $\geq 1.1$ were excluded ($n = 14$ plots). Thus, the final sample size was $n = 376$.

### 2.2.3 | Regression analysis

For the regression analyses, we first performed stratified sampling of the posterior distribution, sampling every 10th iteration, thus obtaining 12,000 posterior samples for each parameter estimate in every community.

Subsequently, we ran intercept-only models (hereafter referred to as null-models), linear models, and in some cases second-order polynomial models for each sample of the posterior distribution (i.e. 12,000 times). We performed our regression analyses testing for a potential habitat effect.

We related (1) the estimates of $S$ and $\sigma^2$ to each other and (2) $S$, as well as the residuals of $\sigma^2$ after accounting for $S$ (hereafter referred to as $\sigma^2_{\text{res}}$), to density (i.e. the number of territories per area) and community biomass (i.e. bird biomass per area), as well as to latitude and NPP. Please see Appendix S4, Table S1 for a full overview of regressions performed.

For visualization of these regressions, we extracted point estimates of the different variables as the mean value of the posterior distribution for a given parameter in a given plot (and as the plot means of the model residuals in the case of $\sigma^2_{\text{res}}$). Also, 95% credible intervals were obtained as the 0.025 and 0.975 sample quantiles of the distribution of model coefficients obtained for each of the 12,000 samples of the posterior distribution.

Note that we also performed simple linear regression for the calculated values of density, community biomass as well as latitude against NPP. In these cases, we calculated 95% confidence intervals.

### 2.2.4 | Model selection

We performed cross-validation to rank the model alternatives. For each sample of the posterior distribution, we randomly selected 2/3 of the plots as our training data and tested the model on the remaining 1/3 of the plots by calculating the root mean square error (RMSE) and mean absolute error (MAE; see e.g. Chai & Draxler, 2014). Finally, we compared the Mean ± SD values of RMSE and MAE of the null-model and the alternative model(s). We also noted the percentage of iterations for which the alternative model was better (note that this percentage must be >50% for this measure to reflect an improvement compared to the null-model). For the simple linear regressions for the measured values of density and community biomass against NPP, we obtained values of RMSE and MAE by leave-one-out-cross-validation (LOOCV). See Appendix S4: Table S1.

## 3 | RESULTS

### 3.1 | Species richness and evenness

We observed a slight positive linear relationship between the variance in the species abundance distribution ($\sigma^2$) and species richness in the community ($S$) in both habitat types (Figure 1 and Appendix S4: Table S1). This indicates a slight decrease in evenness

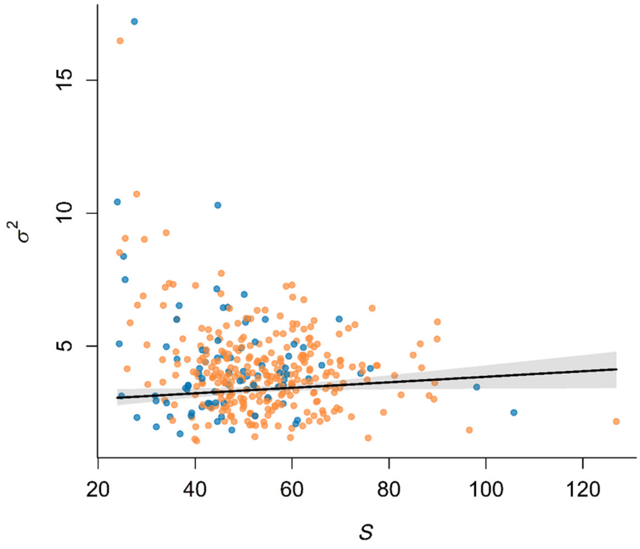

FIGURE 1 The variance ($\sigma^2$) of the multivariate Poisson log-normal distribution as linear function of estimated species richness ($S$) in the community. Plots are divided into open ($n = 289$, orange colour) and forest ($n = 87$, blue colour) habitat. The black regression line indicates no significant habitat effect. The 95% credible interval is added.

as species richness increases; that is we found a slightly increasing dominance of one or few species as species richness increased. The relation did not differ significantly between habitats. However, our simulations show that, for communities of similar structure to that found in our data, such a positive linear relationship between $\sigma^2$ and S can arise even if there is no factual relationship in the underlying data (Appendix S6). Thus, we do not find significant support for any relationship between species richness and dominance or evenness in the communities.

Therefore, we considered it appropriate to extract the residuals from this relationship as described above and continue our analyses with $\sigma^2_{res}$, i.e. the variance of the distribution when accounting for the effect of species richness (further referred to as relative evenness).

## 3.2 | Richness and evenness in relation to density and community biomass

Community biomass showed a positive linear relationship with species richness, with a significantly steeper slope in forest compared to open habitats. Density (i.e. the number of territories per area) showed a slight increase with richness, and intercept differed significantly between habitats (Figure 2a, Appendix S4: Table S1). The relative evenness of the distribution of abundances showed no relationship either with community biomass or density.

## 3.3 | Effects of latitude and productivity

Net primary productivity decreased strongly with increasing Latitude (Open: intercept [SE] = 2.36 (0.11), slope [SE] = −0.03 (0.002) $p > 0.05$, Forest: intercept [SE] = 2.03 [0.16], slope [SE] = −0.02 [0.003] $p > 0.05$), see also Appendix S4: Figure S1. The patterns described below were largely similar when using either latitude, NPP or GPP as predictor. However, NPP was the better predictor where the alternative model was better than the null-model (Appendix S4: Table S1).

Density increased with NPP, with a significant difference in intercept between the habitats (higher density supported in forest habitats; Figure 3a, Appendix S4: Table S1). Community biomass also increased with NPP, with no significant habitat effect (Figure 3b, Appendix S4: Table S1). We found a unimodal (hump-shaped) relationship between NPP and richness, with estimated richness peaking at intermediate levels of NPP, with a significant difference in intercept between habitats (Figure 3c). We found no relationship between Latitude/NPP and relative evenness ($\sigma^2_{res}$) (Figure 3d, Appendix S4: Table S1).

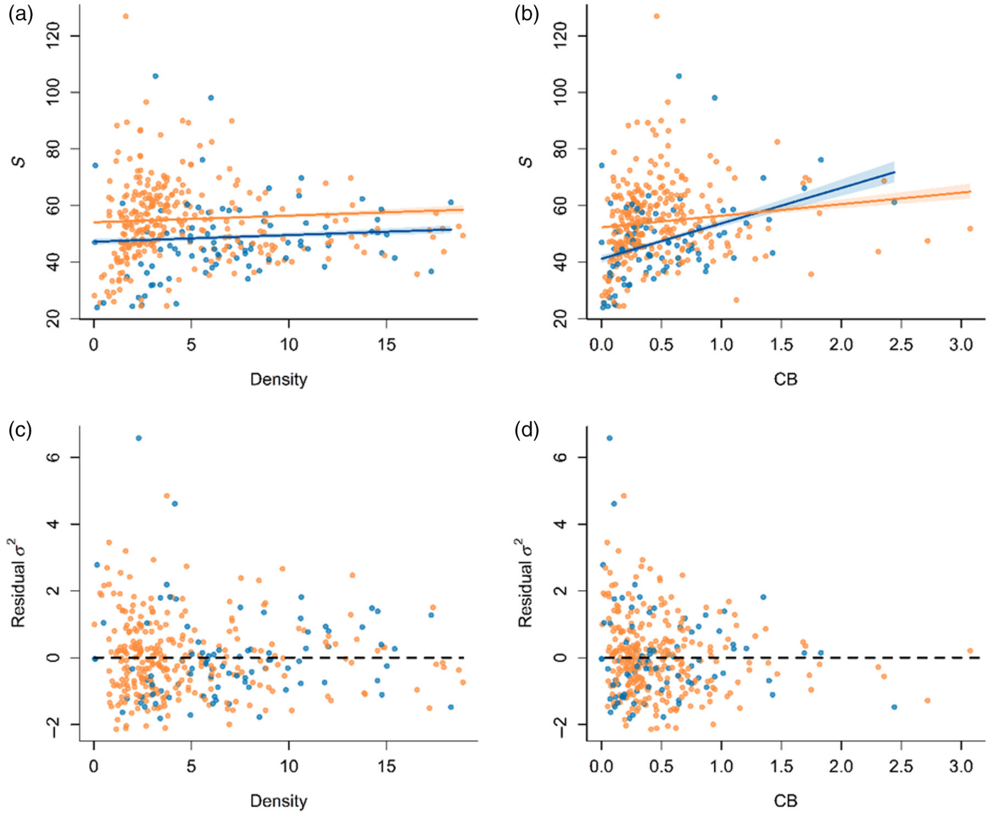

FIGURE 2 (a and b) Estimated species richness (*S*) in the community, and (c and d) relative variance (Residual $\sigma^2$) of the multivariate Poisson log-normal distribution as linear functions of Density and Community biomass (CB). Plots are divided into open ($n = 289$, orange) and forest ($n = 87$, blue) habitats. Dashed regression lines are used for non-significant relationships. Coloured 95% credible intervals are added for within-habitat relationships that differed from the null model.

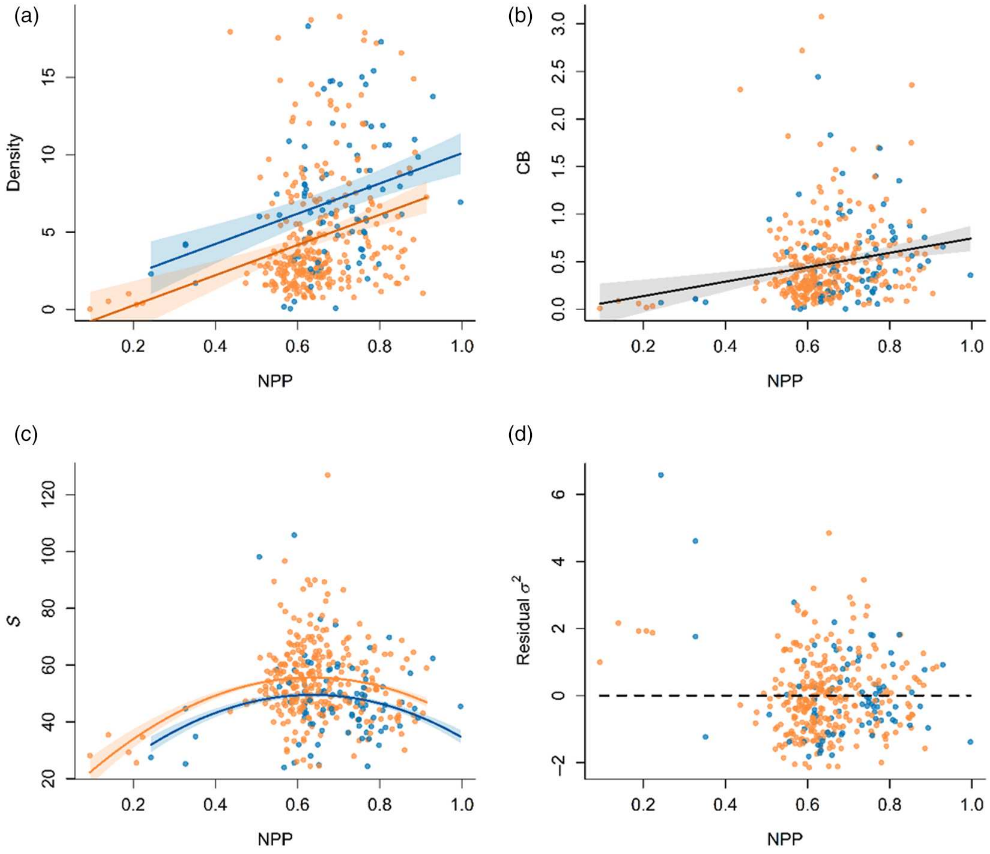

**FIGURE 3** (a) Density and (b) community biomass (CB), (c) estimated species richness (*S*) and (d) relative variance (Residual $\sigma^2$) of the multivariate Poisson log-normal distribution in relation to Net Primary Productivity (NPP). Plots are divided into open ($n = 289$, orange) and forest ($n = 87$, blue) habitats. Black regression lines are used when there was no significant habitat effect, and dashed lines for non-significant relationships. 95% credible intervals are added (coloured if habitat effect is significant, grey if not and absent if the null model was best).

## 4 | DISCUSSION

We did not find strong support for any relationship between richness and evenness. Further, richness and evenness showed distinct responses to various measures of productivity: Richness increased with levels of community biomass, and also slightly with density, while evenness was not influenced by any of these. Since both measures of abundance were explained by NPP, richness, but not evenness, was partially explained by energy-diversity theory. However, richness did not increase linearly with NPP but rather showed a unimodal ('hump-shaped') relationship. Evenness was not related to NPP. In other words, energy-diversity theory alone is not sufficient to explain the observed patterns, and, importantly, the two components of diversity seem to be governed by separate mechanisms.

To successfully study biodiversity patterns across gradients, large-scale, high-quality data are necessary. Here, we utilized the unique data that has been collected on European bird communities by the method of territory mapping (Enemar, 1959), an area-based sampling method where a fixed area is carefully censused at several instances throughout the observation period. Thus, the estimated number of territories is likely to accurately represent the actual number of territories within the sampling area, implying a small observation error. However, the actual number of territories is a stochastic realization (a sample) from the abundance distribution of the larger community, necessitating the use of the Poisson sampling distribution. In addition, we expect that estimates of richness and evenness become more stable when utilizing multiple samples in time to estimate these, as was done here. It is important to note that accounting for autocorrelation (similarity of relative species abundances in time) results in a more accurate estimate of uncertainty.

### 4.1 | The relationship between species richness and evenness

Several studies have investigated the richness-evenness relationship in birds. For instance, Tramer (1969) found relative abundance to be relatively constant across the range of species richness in their study of breeding birds. Later, Cotgreave and Harvey (1994) found the two to be positively related (based on 90 bird communities worldwide), but the measures used for the two components were not mathematically independent sensu Smith and Wilson (1996). Later investigations consistently report a negative relation for birds (Berduc et al., 2015; Bock et al., 2007; Pautasso & Gaston, 2005; Sæther et al., 2013; Symonds & Johnson, 2008). A negative relationship between richness and evenness indicates increasing dominance of one or few species as species richness of bird assemblies increases.

In line with these previous findings, we similarly found a slight positive relation between species richness and the variance in species abundance distribution $\sigma^2$ (Figure 1), indicating a slightly negative relationship between species richness and evenness. We additionally observed a negative relationship between observed species richness and two commonly used measures of evenness, Smith and Wilson's $E_{var}$ (Smith & Wilson, 1996) and Simpson's Evenness (Pielou, 1969; Simpson, 1949), see Appendix S5: Figure S2 and Table S1. However, our simulation study showed that such a relationship can arise even when there is no actual relationship between the variance and the richness in the underlying data (see Appendix S6: Section S1 and Figure S1). Thus, we here cannot conclude that there is any significant relationship between evenness and richness, and we strongly encourage future research to use simulations to verify results, as it seems difficult to produce a measure of evenness that is fully independent of the measure of richness used (Jost, 2010). This is of utmost importance, because our findings indicate that richness does not covary with evenness in a simple way. Thus, our study reinforces the suggestion of previous research to treat richness and evenness as distinct measures of species diversity (e.g. Magurran, 1988; Weiher & Keddy, 1999; Whittaker, 1965).

## 4.2 | Effects of NPP on richness and evenness

In this study, we did not see a one-to-one translation of available energy (NPP) to species richness. Both the levels of biomass supported by the ecosystem (measured as community biomass) and density were explained by NPP (Figure 3a,b), and we observed an increase in species richness with increasing levels of community biomass (Figure 2b), as well as a slight increase with density (Figure 2a). In line with the findings of McNaughton et al. (1989), we found that community biomass was explained by primary productivity (Figure 3b). Such an increase in community biomass with productivity can be caused either by an increase in individuals, or by an increase in body weight. Here, average mean weight of the species in the communities was not significantly related to NPP (intercept [SE] = 0.21 [0.04], slope [SE] = −0.006 [0.06] $p = 0.92$).

An increase in density with primary productivity such as observed here (Figure 3a) points to higher availability of resources such as food and nesting sites at high-productivity sites. This led to a slight increase in species richness in both habitats (Figure 2a).

We observed that the increase in richness with increasing community biomass was stronger in forest compared to in open habitats (Figure 2b), indicating that more complex habitat types may offer a wider range of available niches, or a greater diversity in resources, allowing for higher species richness. This is in line with findings of for example (Lõhmus, 2022a, 2022b), who found density and species richness to be higher in fertile forest habitats compared to less productive sites. Similarly, Hurlbert (2004) found that the relationships between abundance and richness differed between habitat types. In their study of North American birds, richness increased at a faster rate with abundance in deciduous forests compared to in grasslands along a productivity gradient. Also, Dobson et al. (2015) observed spatial covariation in richness with productivity in North American birds, but suggested that this was confounded with habitat complexity, because they found no relationship between the two when monitoring species richness changes over time in plots in which NDVI has declined.

Relative evenness (i.e. evenness after correcting for the slight dependency with richness, $\sigma^2_{res}$) was not influenced by any of the aspects of community abundance (number of territories or observed biomass) in the communities (Figure 2b). Thus, we do not find any support here for a bottom-up regulation of evenness.

## 4.3 | Other effects of latitude on community structure

Energy-diversity hypotheses predict that richness should increase linearly with energy. NPP was linearly correlated with latitude, and both density and community biomass were explained by NPP. However, we observe a unimodal relationship between NPP and richness (see also Appendix S4: Table S1). There was no relationship between NPP and relative evenness (Figure 3d). Thus, the energy-diversity hypotheses alone do not sufficiently explain the observed patterns in richness and evenness along the productivity gradient (Figure 3c and Appendix S4: Table S1).

An unimodal relationship between richness and latitude has also previously been documented for birds. Gaston (2000) studied richness of New World birds along a vast latitudinal gradient, and as expected, found bird species richness to decrease towards both poles, with highest richness in equatorial regions. If our study had included equatorial regions as Gaston's (2000) work did, we might have seen an increase in species richness at those regions which in our study showed a decrease (mid-Europe). When studying the entire gradient from pole to pole, a hump-shaped pattern, with its peak at equatorial areas, is likely perceived due to the striking diversity at this zone, constituting a 'global maximum' in richness. However, as Barthlott et al. (1996) and Barthlott et al. (2005) showed in their studies of plants, species diversity is very closely linked to abiotic factors ranging from climatic conditions to the variety of geological conditions in mountainous areas. Such conditions and factors can create both local and regional diversity minima and maxima. Thus, the hump-shaped pattern we saw in this study may constitute a local richness maxima, which would likely not be visible if equatorial regions were included. It is very important to gain knowledge on local diversity maxima, both in terms of richness and evenness, as this can affect management and conservation decisions.

The other component of species diversity, evenness, was not influenced by productivity levels. We also checked if community evenness (mean values of $\sigma^2_{res}$) differed between the two habitat types, but a one-way ANOVA did not reveal any such difference ($F(1, 374) = [0.004]$, $p = 0.95$). Tramer (1969) suggested that in species such as birds, for which intraspecific density regulation is strong, birth and death rates are relatively stable across generations. He argued that this may lead to similar abundance distributions of the species in different communities. However, we observed quite some variation in the variance of the Poisson-lognormal distributions of the communities (Figure 1), implying differences in the abundance distributions from site to site (which were also observable when visually investigating the time-series data: In some communities, there was a clear dominance of one or few species, while other communities had a quite even distribution of individuals among species). Thus, here we cannot conclude that evenness did not vary among the communities.

Another factor that can influence diversity patterns is the interplay between bottom-up and top-down regulation (Terborgh, 2015, Figure 1). Terborgh (2015) based his work on the observed (often dramatic) effects of both predator removal, but also the presence of superpredators on species diversity. In the absence of predation, oftentimes a previously diverse system is seen to become greatly altered due to increased competition for resources (bottom-up effects). Similarly, introducing a superpredator decreases diversity, driving ecosystems to unrecognizable alternate states (top-down effects). Thus, intermediate levels of predation may be an 'unseen' factor promoting species diversity (Terborgh, 2015).

## 5 | CONCLUSIONS

The study did not find a strong relationship between species richness and evenness in European bird communities. Species richness increased with community biomass and density but was not linearly related to NPP. The unimodal relationship observed between richness and NPP, with a peak at mid-latitudes, suggests that energy-diversity theory alone is insufficient to explain biodiversity patterns. In contrast, evenness was not influenced by any measures of abundance or productivity. Other factors like habitat complexity and the interplay of bottom-up and top-down regulation may also play important roles.

The study highlights the importance of treating richness and evenness as distinct components of diversity, as they appear to be governed by separate mechanisms. Future research should use simulations to verify results, as measures of richness and evenness can be mathematically interdependent.

Overall, the findings reinforce the need for large-scale, high-quality data and a nuanced understanding of the multiple drivers of biodiversity patterns across environmental gradients. Focusing solely on richness or energy-based hypotheses may overlook important aspects of community structure and dynamics.

## AUTHOR CONTRIBUTIONS

Lisa Sandal, Vidar Grøtan and Bernt-Erik Sæther conceived the ideas and designed methodology; Lisa Sandal and Vidar Grøtan analysed the data; Lisa Sandal led the writing of the manuscript. David G. Noble, Johannes Schwarz and Agu Leivits provided the data. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Archived data and model code are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.2547d7x0r (Sandal et al., 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Data distribution.

**Appendix S1: Figure S1.** The distribution of plots across Europe.

**Appendix S1: Figure S2.** Years for which census data were available for the different plots.

**Appendix S1: Table S1.** Habitat categories (UN-LCCS classes) included in the categories 'open' and 'forest' utilized in this work.

**Appendix S2.** Priors.

**Appendix S3.** Model convergence.

**Appendix S3: Figure S1.** Evaluation of MCMC convergence of the model in terms of potential scale reduction factors for the S and $\sigma^2$ parameters.

**Appendix S4.** Model selection.

**Appendix S4: Table S1.** Mean and SD root mean square error (RMSE) and mean absolute error (MAE) of the different models tested, obtained by cross-validation (CV) for each sample of the posterior distribution of the parameter estimates of S and $\sigma^2$ ($n = 12{,}000$).

**Appendix S5.** Supporting information.

**Appendix S5: Figure S1.** The relationship between Net Primary Productivity (NPP) and Latitude.

**Appendix S5: Figure S2.** (A) Smith and Wilson's $E_{\text{var}}$ as well as (B) Simpson's Evenness as linear functions of observed number of species in the communities.

**Appendix S5: Table S1.** Parameter estimates of the models depicted in Appendix S5: Figure S2.

**Appendix S5: Figure S3.** The relationship between Net Primary Productivity (NPP) and Gross Primary Productivity (GPP) during the breeding season (April–July).

**Appendix S6.** Simulation study.

**Appendix S6: Figure S1.** The relationship between (A) true values of $\sigma^2$ and S used in the data simulation, (B) estimated values $\sigma^2$ and S using the simulated data, (C) Smith and Wilson's $E_{\text{var}}$ as well as (D) Simpson's Evenness and the 'observed' number of species obtained from the simulated data.

**Appendix S7.** Species list.

**Appendix S7: Table S1.** List of bird species encountered across all plots and all years in the presented study ($n = 252$ species).

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