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Sandal Lisa

Spatiotemporal dynamics of avian communities

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Norwegian University of Science and Technology
Thesis for the Degree of
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Trondheim, November 2023

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"What I see in nature is a magnificent structure that we can comprehend only very imperfectly, and that must fill a thinking person with a feeling of humility."

~ Albert Einstein

Contents

List of Papers

The thesis includes three papers:

I. Sandal, L., Grøtan, V., Sæther, B. E., Freckleton, R. P., Noble, D. G., & Ovaskainen, O. (2022). Effects of density, species interactions, and environmental stochasticity on the dynamics of British bird communities. *Ecology*, *103*(8), e3731.

II. Sandal, L., Sæther, B. E., Freckleton, R. P., Noble, D. G., Schwarz, J., Leivits A., Grøtan, V. (2023). Species richness and evenness of European bird communities show differentiated responses to measures of productivity. (Manuscript in review)

III. Sandal, L., Sæther, B. E., Grøtan, V. (2023). Patterns in bird community dynamics affect variation in species abundance distributions. (Manuscript)

Declaration of contributions:

Paper I. LS, BES, VG and OO conceived the ideas and designed methodology; LS, OO and VG analyzed the data; LS led the writing of the manuscript. DGN provided the data. All authors contributed critically to the drafts and gave final approval for publication.

Paper II. LS, VG and BES conceived the ideas and designed methodology; LS and VG analyzed the data with input from BES; LS led the writing of the manuscript. DGN, JS and AL provided the data. All authors contributed critically to the drafts and gave final approval for publication.

Paper III. LS, VG and BES conceived the ideas and designed methodology; LS and VG analyzed the data with input from BES; LS led the writing of the manuscript. All authors contributed critically to the drafts.

Introduction

As human beings we have been given a unique position of responsibility in taking care of nature—the foundation of our existence in this world that we share with innumerable other living entities in different forms of life. In order to adequately meet this responsibility, knowledge about the structuring forces and drivers behind the observable is essential. Within the field of biology alone, there are many levels at which this knowledge is sought—from the molecular level to the level of the entire ecosphere (Odum & Barrett 1971).

In our search for knowledge, community ecology is a fundamental level of investigation due to its significance in understanding the co-existence of species inhabiting a given area (Vellend 2010; Morin 2011). Community ecology serves as a bridge between research on the level of individual species and larger-scale ecological studies. It is an instance of research at which it is still possible to retain valuable species-level information, at the same time broadening the perspective to gain knowledge on more general patterns in nature. As such, studies within the field of community ecology are fundamental for conservation efforts.

Nature is inherently complex, and we may never be able to fully describe and capture the intricate interplay of biotic and abiotic factors that takes place on so many different levels. However, we may be able to approximate the dynamics and patterns of nature using models. Models provide a valuable tool for simplifying complex ecological systems and making them more feasible for analysis (Hall & Day Jr 1977; Schmolke *et al.* 2010). Although models are certainly only a crude "sketch" of natures' complexity, still, they are powerful tools that help us understand the general principles and mechanisms that underly the observed patterns. This is essential for making predictions about how nature might respond to future changes such as global warming and increased anthropogenic land use and modification. Models help us to identify relevant variables and relationships, which in turn is the foundation for the development of management strategies (Cardinale *et al.* 2012; Getz *et al.* 2018; Schuwirth *et* *al.* 2019). Obviously, the accuracy and reliability of models heavily rely on the quality of the data used as input (e.g., Aubry, Raley & McKelvey 2017; Van Eupen *et al.* 2021). Models are only as good as the data they are based on, and the selection of appropriate variables as well as accurate measurements are essential for robust model performance.

Communities

Krebs (1972) defined a community in very general terms as being "an assemblage of populations of living organisms in a prescribed area or habitat". This is a broad definition, based on which decisions can be made on what area and species assemblage should be studied in a given context. There are numerous different definitions of what a community is (Morin 2011). In the broadest sense, a community could be defined as all species persisting together in a certain area. However, collecting high-quality data on all species of a community (including bacteria, protozoa etc., for which taxonomy still remains poorly known (e.g., Hughes *et al.* 2001), at this stage, must be considered impossible for most real communities. Therefore, community ecologists often focus their attention on subsets of communities, for example guilds, functional groups, taxocenes or trophic levels (Morin 2011).

Community ecology began as a descriptive science, primarily concerned with listing and identifying the different species in different locations, as well as describing the conspicuous patterns that biodiversity exhibits (e.g., Clements 1916; Elton 1966). For instance, especially in temperate habitats, a few species often exhibit a clear dominance in abundance compared to others (Morin 2011). Also, for instance there are noticeable patterns in species richness along the latitudinal gradient (Rohde 1992; Hillebrand 2004), and in the succession of species in communities over time (Anderson & Kikkawa 1986; McCook 1994). To this day, the search for an understanding of the processes that shape community structure and dynamics, including the species' abundances and their distribution is central to community ecology. Although many hypotheses have been proposed and explored, there is still work to be done before we can claim that we have found the definite answers to these questions. Perhaps due to the overwhelming complexity of the task at hand, and the amount and quality of data required to transcend the often very local nature of community ecology studies, Lawton (1999) declared the field of community ecology to be “a mess”. However, recently, community ecology has made significant methodological and conceptual advances, discussed in the paragraph below (see e.g., Morin 2011; Vellend 2016; Leibold & Chase 2017). Factors such as considerable progress in computational techniques, development of multivariate statistical tools and increased data sharing among researchers all contribute favorably to a brighter outlook on our possibilities in answering long-standing questions in community ecology (Michener 2015; Shoemaker *et al.* 2021; van der Veen 2022).

Community data and analyses

Data on species communities can be collected either in a natural setting or by recording the results obtained from experiments conducted either in the field or in the laboratory (Sutherland 2006). Some examples of experimental approaches to studying communities include translocation or transplanting of individuals in order to study the effect of invasive species on biodiversity or the effect of removing a predator/herbivore (e.g., Maron, Pearson & Fletcher Jr 2010; Sørensen *et al.* 2018). Also, for example specific environmental variables can be manipulated in order to study the effect of e.g. extreme weather phenomena or increased temperature on vegetation (e.g., Walker *et al.* 2006; Le Moullec *et al*. 2021).

Community data can be measured in different units, such as for instance as presence-absence data, counts or cover percentage (in plant communities). Although often not feasible, counting or mapping every single individual can sometimes be done, for instance in experimental or laboratory settings (e.g., Brook, Grace & Hayward 1981; de Omena, Srivastava & Romero

2019), or in bird communities during the breeding season when individuals are territorial (territory mapping; (Enemar 1959, Sutherland 2006)). However, in most cases, only a sample of the community can be taken, which is assumed to represent the community as a whole. Many species are rare (i.e., they have a small relative abundance), and a commonly observed pattern is that the number of unique species in the sample grows with increasing number of individuals sampled, and even large samples will tend to contain some species with only one or a few sampled individuals. The real number of species in the community is mostly larger than the number of species sampled, and statistical techniques such as species rarefaction curves are often used to estimate the actual number of species in the community based on a sample of the community (Gotelli & Colwell 2001).

Methods such as line transects (sampling along a defined route), point counts (regularly sampling at specific localities) or different types of trapping methods (for instance when studying insects) can all provide valuable samples of the community (Sutherland 2006). Cover percentage can be measured using quadrat sampling, and if the research question requires only presence-absence data, citizen science data (e.g. Dickinson, Zuckerberg & Bonter 2010; Krabbenhoft & Kashian 2020) or new promising methods such as the use of DNA-barcoding to identify species in samples (e.g. Yu *et al.* 2012; Deiner *et al.* 2017), automatic species recognition from acoustic recordings (e.g. Wood, Gutiérrez & Peery 2019; Desjonquères, Gifford & Linke 2020) or camera trap images (Tabak *et al.* 2019) can be explored.

The collected data can subsequently be analyzed in many different ways, depending on the research question. In its most simple form, community data can be presented for instance as species lists or cover percentages. The use of biodiversity indices to describe communities is very prominent (Iknayan *et al.* 2014; Heydari, Omidipour & Greenlee 2020). Different indices are used to measure local and regional diversity as well as the turnover in species composition between communities either in space or time (α-, β- and γ- diversity respectively), such as for instance Shannon’s and Simpson’s Diverstiy indices (α and γ diversity), Sørensen or Jaccard Similarity Indices, Bray-Curtis Dissimilarity Index (β diversity) etc. (see e.g. Iknayan *et al.* 2014; Moreno *et al.* 2018; Heydari, Omidipour & Greenlee 2020). However, much information is lost when summarizing communities solely with single indices. An alternative or complementary way to study communities in more detail is provided by analyzing their species abundance distribution (SAD) (May 2011). The use of SADs in community inference dates back to the important contributions by Fisher, Corbet & Williams (1943) and Preston (1948). SADs can be used for instance to assess the level of rarity of endangered species (McGill 2011), or to estimate the richness and evenness of communities (Sæther, Engen & Grøtan, 2013). Also, monitoring changes in a communities’ SAD over time can serve as an early warning for extinction risk (Hågvar 1994; Mouillot *et al.* 2013), and the variance of different samples of SAD’s in time can be decomposed to analyze the relative contribution of different intrinsic and extrinsic factors to community dynamics (Engen *et al.* 2002).

Another class of methods commonly used in community inferences is ordination. Ordination provides a means to reduce complex ecological datasets into a few key axes representing major trends (unconstrained ordination, such as e.g. Principal Component Analysis). Ordination can also be used to link community composition to environmental factors (constrained ordination, such as e.g., Canonical Correspondence Analysis) (see e.g. Palmer 2004 for an overview on ordination methods).

Following the rapid methodological and technological advances in recent time, the use of model-based approaches has become more integrated in community ecology (Warton *et al.* 2015). This is reflected for instance in the way various community measures are being analyzed; for example, generalized linear mixed-effect models (GLMMs) can be used to model biodiversity indices as functions of different environmental variables (e.g., Winkler *et al.* 2016; Hamza & Hanane 2021), and a recent study used GLMMs to investigate measures of community sensitivity and resistance to environmental perturbations (Sæther, Engen & Solbu 2023). In addition (and often hand in hand), the development and use of multispecies models is becoming increasingly established. For instance, Joint Species Distribution Models (JSDM), which can be viewed as extensions of GLMMs (i.e., treating the entire community data as the response variable), constitute an important advancement in community ecology.

Especially the introduction of latent variable models into community ecology models (also known as generalized linear latent variable modeling, GLLVMs) is a key development, as it greatly reduces the dimensionality of multispecies analyses (JSDMs with latent variables can be viewed as model-based ordinations). The GLLVM framework is now commonly used in JSDMs, making it possible to study real species communities with hundreds of species (e.g. Warton *et al.* 2015a; Thorson *et al.* 2016; Ovaskainen & Abrego 2020; van der Veen 2022). Recently, GLLVMs have also been used to expand traditional ordination methods (van der Veen *et al.* 2023). JSDMs can be used to study co-occurrence patterns after accounting for species' similar or dissimilar responses to environmental variables (e.g., Pollock et al. 2014; Tikhonov et al. 2017; D'Amen et al. 2018). They are also used to study the impact of phylogeny and traits on community structure (e.g., Morales-Castilla et al. 2017; Ovaskainen et al. 2019; Violet et al. 2022). An extension of JSDMs that can be fitted to time-series data constitutes a further milestone in the development of these models, as it allows for the estimation of species interactions directly from species abundance data in previous years instead of from the residual covariance matrix, greatly enhancing the reliability of the estimates (Ovaskainen *et al.* 2017b; Ovaskainen & Abrego 2020; Sandal *et al.* 2022). Some JSDM utilize Bayesian inference, using the Markov chain Monte Carlo (MCMC) method to fit the model to the data (see e.g., Warton *et al.* 2015a; Ovaskainen & Abrego 2020). The use of Bayesian inference in community ecology in general is another exciting and promising, flexible tool allowing for the use of complex ecological models (e.g., Ellison 2004; Warton et al. 2015b)

Community ecology methodology is being developed on multiple fronts. For instance, structural equation modeling (SEM) also constitutes a noteworthy contribution. SEM can be used to investigate hypothesized direct and indirect relationships (again, Bayesian approaches can be useful, especially in complex, non-linear cases, see e.g., Palomo, Dunson & Bollen 2007; Muthén & Asparouhov 2012), and has for instance been used to study relations between species of different trophic levels along with different environmental variables influencing them (e.g., Riginos & Grace 2008; Du *et al.* 2015; Mamet *et al.* 2019). SEM has also been used to relate biodiversity indices to environmental variables (Santillán *et al.* 2020). Recent advancements in the use of artificial intelligence in ecological studies (e.g., Rammer & Seidl 2019; Hsiang & Hull 2022; Stupariu *et al*. 2022) also have great potential as a future tool for inferences.

Identifying key drivers of community dynamics

In this thesis, we go back to very basic community ecology questions and try to answer them in a more general way by applying multivariate statistical models to high-quality, long-term, large-scale bird abundance data and utilizing Bayesian inferences. The first step in such an approach must be to identify key processes that need to be taken into account when building the models that attempt to describe the observed data. In other words, what structures communities? Obviously, we cannot take into account (and we have most likely not identified) all potential structuring factors, so the question is, which of these are necessary to include to adequately describe the observed? In this connection, Hubbel (2001) put forward his neutral theory of community ecology, proposing that biodiversity emerges and is organized at random. The theory assumes species to be identical, that is, on a per capita basis, species are equal in demographic variables such as growth rates, their ability to colonize a new area etc. Temporal and spatial variation in species abundances and composition is assumed to arise by chance migration from a regional species pool, as well as demographic stochasticity (which may also cause random extinction of species) (Hubbell 2001; Chave 2004). While natural communities likely are not maintained solely by random processes, the neutral theory is a highly valuable contribution to ecology, because in the overwhelming complexity of factors to take into account when dealing with communities, it serves as a null-model for evaluating the roles of other, deterministic processes (Ovaskainen & Abrego 2020).

In contrast to neutral theory, the traditional view on communities is a niche-based one. Hutchinson (1957, 1978) defined the fundamental niche of a given species as the sum of all environmental variables and resources required for that species to survive and reproduce. Further, species are thought to coexist within a certain area by partitioning resources and avoiding direct competition, either through differences in their ecological niches or through specialized adaptations or behaviors, such as for instance between-species differences in their timing of feeding or reproduction. The resulting actual dimension that the species can occupy in the presence of biotic interactions such as competition, predation, mutualism etc. is called a species' realized niche. As Leibold and McPeek (2006) pointed out, the future of community ecology doesn't lie in arguing about which of the two schools of thought (neutral vs. niche theory) is correct, but rather focusing our attention on synthesizing niche and neutral perspectives. Although this thesis builds upon a niche-based view of communities, it also recognizes the importance of stochastic processes. Thus, we herein explore the potential importance of both deterministic and stochastic processes in bird communities. Rather than strictly adhering to one paradigm or another, we here simply attempt to incorporate the knowledge that we as ecologists have gained from studying population dynamics and ask if the same mechanisms are acting also on the community as a whole. Single-species dynamics are relatively well understood, and different key deterministic and stochastic processes (outlined below) have been identified to be of importance on the population level. There is still limited knowledge about the potential significance of different such processes at the community level (e.g., Kinzey & Punt 2009; Engelhardt, Neuschulz & Hof 2020), and thus we here make an attempt to broaden our understanding in that regard.

Birds as study system

Birds comprise an exceptional study unit for numerous reasons. Firstly, birds are extensively studied. Some of the reasons for the great research interest in birds is that they are easily observed- they are active during daytime, easy to detect (birds are often conspicuous and highly vocal), relatively easy to trap and mark with leg rings, etc. (e.g., Feduccia 1978; Busse & Meissner 2015). Territoriality during the breeding season is widespread in birds (Nice 1941), creating an ideal situation for detailed territory mapping (Enemar 1959), yielding exceptionally high-quality count data (see more details in the Methods section below). Due to the extensive data collected and continuous monitoring effort being done relative to other taxa, birds also serve as indicator species of the general 'health' of ecosystems (e.g., Mekonen 2017; Fraixedas et al. 2020). The great interest in birds makes it possible to study for instance the impact of human disturbances such as pollution, habitat fragmentation and climate change on bird communities (e.g., Brotons *et al.* 2010; Halstead *et al.* 2019; Sander & Tietze 2022), with implications also for other taxa.

Another feature which sets birds apart from most other living entities is their high dispersal ability (Paradis *et al.* 1998). Many birds are migrants, sometimes covering vast distances every year (e.g., Mouritsen 2018). The high mobility of most birds makes dispersal limitation in their abundance distributions less pronounced than in many other taxa (with notable exceptions; for instance, some tropical forest birds have been found to be unable to cross even seemingly insignificant barriers between habitat patches, see e.g., Moore et al. 2008). For instance, Qiang (2009) found β-diversity to be consistently lower for birds and mammals both at regional and global extents (i.e., species composition across space was more similar) than for reptiles and amphibians. Similarly, Steinitz *et al.* (2006) confirmed that, as expected, the decay in species similarity between communities was significantly faster in mollusks compared to in birds within the same geographic extent. Thus, bird distribution patterns might be relatively more influenced by other factors, such as environmental constraints, interspecific interactions or stochasticity (e.g., Alatalo 1982; McCain 2009; Campbell, Witham & Hunter Jr 2010), see paragraph below. The main environmental limitations for birds globally seem to be temperature and water variables, as summarized by McCain (2009) in an extensive review.

From populations to communities

Species display a wide range of differences in their respective dynamics, such as for instance differences in life histories, intrinsic rates of increase, dispersal rates etc. (e.g., Roff 1992; Clark 2009; Purves & Turnbull 2010). In addition to between-species differences in their dynamics, there can also be within-species variation across regions (e.g., Menges & Dolan 1998; Jongejans *et al.* 2010). Despite such between-species differences, there are some processes which emerge as important across species, outlined below.

Time-series studies of single or few species have demonstrated that density dependence, which is the impact of current or past population densities on the population growth rate, is an important process affecting population dynamics. (e.g., Royama 1992; Lande, Engen & Saether 2003). Density dependence may occur through intraspecific competition for limited resources (e.g., Hansen *et al.* 1999; Amundsen, Knudsen & Klemetsen 2007) or through interference competition that excludes individuals' access to space (e.g., Moksnes 2004; Denac 2006). Brook and Bradshaw (2006) demonstrated that 75% of 1198 invertebrate and vertebrate species, including birds, showed intraspecific density dependence in their per-capita growth rates.

Population fluctuations are additionally influenced by environmental stochasticity, i.e., between-year variation in populations' expected survival and fecundity, caused by random variation in the environment such as for instance weather, pollution, or habitat loss, leading to fluctuations in population size (Lande 1993; Lande, Engen & Saether 2003). Environmental stochasticity tends to reduce the long-run population growth rate (Lewontin & Cohen 1969; Lande, Engen & Saether 2003) and has been shown to strongly affect many species (e.g., Dobinson & Richards 1964; Grant 1986; Grøtan *et al.* 2009). Environmental stochasticity affects individual species in varying degrees due to specific traits and life history characteristics, such as differences in habitat preferences, feeding behavior, or reproductive strategies (Lande, Engen & Saether 2003; Morris & Doak 2004). The responses of species to the variation in the environment may thus be correlated to a larger or lesser extent, depending on their ecological similarity. A high degree of synchrony in species' abundance fluctuations can negatively influence the long-term persistence of communities (Harrison & Quinn 1989; Heino *et al.* 1997).

Demographic stochasticity, within-year variation between individuals in survival and fecundity (MacArthur & Wilson 1967; Lande, Engen & Saether 2003) is also widely accepted as being an important process in population dynamics. Its impact is most pronounced at low population sizes, where individual fitness variation reduces the long-term population growth rate and increases the risk of extinction (e.g., Lande, Engen & Saether 2003; Melbourne & Hastings 2008).

Apart from such mechanisms acting on the level of the individual species, when moving to the level of the community, it is obviously also necessary to consider the context in which the species co-exist. This involves direct and indirect interaction among the species sharing a common space, which is considered an important structuring force in natural communities (Elton 1946; Hardin 1960; Cody & Diamond 1975). In this thesis, we evaluate the role of species interactions in the community in terms of interspecific density dependence—i.e., as the effects of the changes in one species' abundance on that of other species, a mechanism considered important in regulating species abundances (e.g., Ovaskainen *et al.* 2017b).

Additionally, movement can greatly influence occurrence patterns (Wiens 1989; Martin, Pearce-Higgins & Fahrig 2017). For instance, interspecific interactions can affect the abundances and distribution of species not only locally, but on a larger spatial scale as well (Gotelli, Graves & Rahbek 2010; Araújo & Rozenfeld 2014). Thus, a set of local communities can be linked together by dispersal in what is called a metacommunity (Holyoak, Leibold & Holt 2005).

Processes such as those discussed above are the "building blocks" underlying different observed patterns that give rise to classic community ecology theory. In this thesis, we study key processes driving community dynamics, allowing us to relate our findings to such theories. For instance, following classic Lotka-Volterra theory, intraspecific competition must be stronger than interspecific competition for species to be able to coexist in the long run without extinction (see e.g., Chesson 2000), and thus determining the relative contribution of intra- and interspecific competition to community dynamics contributes to a better understanding of the existing theory. Likewise, estimating the influence of different components of environmental stochasticity (i.e., environmental stochasticity affecting all species in the same way, versus stochasticity influencing different species in different ways) is relevant in the study of community stability, as synchronized responses of different species to environmental perturbation can have a destabilizing effect on communities (De Mazancourt *et al.* 2013; Valencia *et al.* 2020). Species diversity is, as mentioned, central in community ecology studies, and thus, careful estimation of its components can shed new light on long-standing hypotheses such as energy-diversity theory (predicting that the more energy is available in the ecosystem, the more species can be sustained by it, see e.g., McNaughton et al. 1989; Rosenzweig & Abramsky 1993; Srivastava & Lawton 1998)

Spatial and temporal context

As briefly touched upon in the previous paragraph, the spatial and temporal context in which ecological studies are performed is highly relevant, as it affects the patterns which can be perceived (e.g., Allen & Hoekstra 1991; Levin 1992; Dornelas *et al.* 2013; McGill *et al.* 2015). Variability in time and space is an inherent characteristic of nature (Sousa 1984). Community dynamics exhibit spatial and temporal variability due to a wide range of abiotic and biotic factors, such as for instance species' tolerance ranges, anthropogenic and natural disturbances, changes in environmental conditions, disease outbreaks, increased competition over resources, arrival of invasive species etc. (see e.g. Sousa 1984; Ricklefs 1987; Kolasa, Hewitt & Drake 1998; Brown 2014). Therefore, a comprehensive understanding of community level processes ideally necessitates study across large spatial and temporal scales (Ives *et al.* 2003; Magurran 2007; Magurran *et al.* 2010). This is, of course, not an easy task, as the community time-series data of sufficient length, quality and spatial extent ideally needed is very rare (Wolfe *et al.* 1987; Magurran *et al.* 2010). Nevertheless, in a world of increasing sharing of data between researchers much can be achieved in this regard (Farley *et al.* 2018; Kühl *et al.* 2019; Runting *et al.* 2020; McCrea *et al.* 2023).

Aims

My thesis aimed to address key questions in community ecology by investigating the drivers of community changes over time and space using large-scale, long-term time-series abundance data on European bird communities. By utilizing multivariate statistical methods and modeling approaches, we investigated how the composition and dynamics of temperate bird communities in time and space are influenced by potentially important structuring forces such as intra- and interspecific density dependence as well as common and species-specific stochasticity. We also examined how species diversity changes along ecological gradients related to productivity. Throughout all three papers, we also investigated between-habitat differences in the observed patterns; more specifically, we made a distinction between simpler, open habitat types, and more complex, forest habitat types.

We approached these questions from slightly different angles throughout this work as follows:

Paper I

The aim of paper I was to increase our understanding of the drivers of community changes over time occurring at different spatial scales using unique large-scale, long-term time-series data on British bird communities. We used a Joint Species Distribution Model, taking into account both abiotic and biotic processes in an integrated way, to examine the relative contribution of intra- and interspecific density dependence at different spatial scales, as well as the influence of environmental variables, to spatio-temporal variation in abundance. Accounting for species interactions is computationally intensive and may lead to overparameterization, and we here investigated to what extent the inclusion of species interactions improved model performance.

Paper II

Species diversity is of great importance for many aspects of ecosystem structure and function, and thus we need to understand what maintains and supports it. In paper II, we investigated how the two components of species diversity, namely species richness and evenness, are related to each other as well as to different measures of productivity. We applied multivariate Poisson log-normal distributions to long-term time-series data on European bird communities, allowing us to estimate the variance of the log-normal species abundance distribution, which acts as an inverse measure of evenness, as well as species richness. Using these estimated parameters, we investigated the relationship between richness and evenness, as well as their potentially differentiated responses to net primary productivity, territory densities and community biomass along a latitudinal gradient in European bird communities.

Paper III

In paper III, we utilized the multivariate Poisson log-normal model from paper II and based on a theoretical framework addressing the underlying mechanisms producing a log-normal species abundance distribution, we were able to decompose its variance into contributions of ecological heterogeneity as well as species-specific and common stochasticity. The aim of this study was to shed light on the mechanisms structuring European bird communities in two major categories of habitat type (open and forest habitat types), reflecting different degrees of habitat complexity, by the use of species-abundance distributions fit to time-series data. The increasing concern regarding biodiversity loss emphasizes the necessity to understand temporal biodiversity changes. For instance, if effects of ecological heterogeneity among species are large compared to effects of noise on fluctuations of abundance, this will lead to a stable community structure with little temporal turnover in relative abundances of species. On the other hand, if species abundances are highly influenced by noise acting independently among species and relative effects of ecological heterogeneity are small, the community correlation will decay more quickly over time.

Methods

The overall recurring theme in this thesis has been to apply and develop novel multivariate statistical tools to utilize the unique wealth of ecological information stored in long-term, large-scale community time-series count data (described in detail below). There are several important advantages of our approach which make this work an important contribution to the ecological literature.

Firstly, community inferences are often performed on "snap-shot" data, i.e., on data gathered at only one point in time. While such studies are very valuable, still, we know from the study of time-series data of single species how variable species abundances are over time. Thus, such "snap-shot" data can only give us an incomplete picture (e.g., Recher & Gebski 1990; Adamík & Kornan 2004). On the other hand, studies that have monitored communities over time are often conducted at one single location. This approach, again, while very valuable, will not give us sufficient information on the generality of the observed patterns, nor on how community drivers might change across space due to e.g., differences in climatic or geophysical conditions. Moreover, count data, such as used herein, has several advantages over presence-absence data which is often used in ecological studies. One such advantage is that count data provide more detailed and precise information about the abundance of the species within a given area and/or time period. Another advantage is that count data retains variability, which is valuable for detecting patterns and relationships in ecological systems.

Secondly, recently, there have been significant advances in statistical and mathematical tools that can be utilized in our inferences within the field of community ecology (Shoemaker *et al.* 2021; van der Veen 2022). Utilizing and continuing to develop such tools may seem daunting, as, by nature, dealing with multivariate analyses is a complex matter. However, the reward in terms of increased knowledge about, and insights into, the processes that govern natural communities is great. In the following, I will give a short presentation of the data underlying my work, as well as a brief summary of the methodology applied and developed in the three papers.

Data

Territory mapping data

Birds, due to their relatively "outgoing" behavior and charming features, have always been endearing to biologists and the general populace. Hence, many dedicated people have over decades collected detailed data on these animals, sometimes using very rigorous sampling protocols. Throughout the thesis, the basis for our analyses was territory mapping data collected by the method developed by Enemar (1959) of bird communities in Europe. In this area-based sampling method, a complete census of a fixed area is performed at several instances during each years' observation period. This sampling method practically removes uncertainty due to differences in sampling intensity, and furthermore gives a uniquely precise and complete observation of the species abundance distribution. The result obtained from this strenuous method is of very high quality. In my thesis, I have had the great fortune to be allowed to work on bird data obtained by such territory mapping, not only for one or a handful of communities, but for hundreds of communities across numerous European countries. Therefore, throughout this thesis, I have felt confident that the foundation for our inferences is solid.

Because of differences in the methods used in our three papers, the data selection varied between the first and the last two papers. In paper I, we applied a JSDM to the entire data set, and therefore, some data selection criteria were necessary in order to ensure a minimum input quality. Therefore, we only included data from plots monitored continuously for ≥ 10 years across the UK, and excluded species observed in less than 30% of the plots. Thus, the data set underlying the analyses performed in paper I was comprised of community count time-series of 10-36 years, monitored between 1965 and 2002, from a total of 121 plots (68 farmland and 53 woodland plots).

In paper II and III our research questions focused on within-community patterns over time and relating these estimated parameters to spatial gradients. Consequently, the data selection also differed. Here, we included data from plots monitored for ≥ 6 years across Europe. 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, e.g., through the influence of demographic stochasticity. The dataset utilized in these two papers encompassed n=376 plots (open habitat: n=289, forest habitat: n=87) monitored for 6-50 years, censused between 1950 and 2018.

Other ecological data

Additionally, for paper I, we accessed local monthly temperature and precipitation data for each plot from the Met Office UKCP09 databases (Jenkins, 2007; MetOffice, 2017).

For paper II, we collected body mass data from Dunning Jr (2007), to obtain a measure of community biomass per area. Additionally, to obtain an estimate of net primary 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).

For both paper II and III, we utilize land cover data in order to determine habitat type for each plot. For this, we accessed the European Space Agency's Climate Change Initiative (ESA CCI) annual landcover maps from 1992-2015 with 300 m resolution (https://www.esa-landcover-cci.org/) (ESA 2017). 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/). Subsequently, we extracted each year's dominant landcover class for each plot with a buffer of 300 m around the coordinates and utilized this information to divide the plots into two rougher categories: “open” and “woodland”, reflecting simpler and more complex habitat types, respectively.

Statistical analyses

In all three papers of my thesis, the application of statistical models that account for the joint dynamics of multiple species in ecological communities is central. We approached our investigations by the use of two major types of models, namely Hierarchical Modeling of Species Communities (HMSC; a JSDM) and a multivariate Poisson log-normal model. Although there are differences in the specific assumptions and implementations of these models, they also have much in common. Firstly, both methods adopt a multivariate statistical approach, considering multiple species simultaneously. Secondly, both approaches incorporate hierarchical structures to account for the nested nature of ecological data, e.g., multiple sampling sites and/or repeated measurements over time. Such hierarchical modeling allows us to account for shared information among species, including potential autocorrelation in time and space.

Paper I

In paper I, we analyzed the data with HMSC, using the implementation for time-series data by Ovaskainen et al. (2017). The time-series HMSC jointly models the species count time-series data of the entire community within a Bayesian hierarchical framework. HMSC is a powerful tool to investigate species interactions: Especially when working with time-series data, species interactions can be inferred as responses to species abundances in previous years, rather than from the residual covariance matrix as is done for “snap-shot” data (Mutshinda, O'Hara & Woiwod 2009; Ovaskainen *et al.* 2017a). This approach greatly enhances the reliability of the estimated interactions. Still, estimating the interaction coefficients for each pair of species can be challenging, as it requires a large amount of data, and therefore, we here evaluated if including species interactions to the model increased model performance.

The foundation of the time-series HMSC is a first-order multivariate autoregressive [MAR(1)] model, a tool used to infer strengths of both between- and within-species interactions (Ives et al., 2003; Novak et al., 2016; Wootton & Emmerson, 2005), specified as follows:

$$y_{i,t} = c_i + \sum_{j=1}^{m} \alpha_{i,j} y_{j,t-1} + e_{i,t}, \tag{1}$$

where $y_{i,t}$ is the log-abundance of species i at time t. c_i denotes the intercept, and $\alpha_{i,j}$ is the interaction coefficient, and $e_{i,t}$ is the noise term. MAR(1) models can be used as relatively simple approximations to complex natural systems, and essentially represent multispecies Gompertz dynamics (i.e., a species' population growth is assumed to be exponential but gradually slows down as the population approaches its carrying capacity) (Ives et al. 2003, Certain et al. 2018).

In the HMSC framework, this model is built for all species simultaneously. In vector form, for all species, eqn. 1 can be written as:

$$\boldsymbol{y_t} = \boldsymbol{c} + \boldsymbol{A}\boldsymbol{y_{t-1}} + \boldsymbol{e_t} \tag{2}$$

Assuming a normal distribution of the data on the log-scale, the standardized log-abundance of species *i* in plot p at time *t* is modelled as a draw from a normal distribution:

$$y_{ipt} \sim N(L_{ipt}, \sigma_i^2), \tag{3}$$

with mean determined by L_{ipt}, the linear predictor of the log-abundance, and variance σ_i^2. The linear predictor includes a fixed (L_{ipt}^F) and random (L_{ipt}^R) term, as well as some residual error. The fixed part is further decomposed into an environmental term (L_{ipt}^E) and a species association term (L_{ipt}^A).

Technically speaking, when applying the time-series HMSC, the response variable is the entire matrix of community time-series data from all plots and at all points in time. As predictor variables, we included the densities of the species in the previous year (in different ways, as described below), species- and site-specific temperature and precipitation data, as well as area and habitat type. We utilized a sliding time-window approach (van de Pol *et al.* 2016) to identify the critical time-window during which temperature and precipitation influence the abundance of each species the most. We included plot as a spatially explicit random effect, and year as a temporally explicit random effect. Here, we modelled species interactions in 3 different ways and compared explanatory- and predictive power to a model excluding interactions. In the second variant (the first being the variant excluding interactions), we estimated the full matrix of species-to-species interaction coefficients by including as predictors the densities of all the species in the previous year. The diagonal elements of this matrix (also estimated in the first model variant) model the intra-specific density dependence. In the third variant, we assumed most species interactions to be zero, using a variable selection approach to identify non-zero interactions. In the fourth variant, we used a latent variable approach wherein species are assumed to contribute to one or more “community-level drivers”, defined as linear combinations of species densities (Ovaskainen *et al.* 2017a).

To examine at which spatial scale intra- and interspecific density dependence might influence local population sizes the most, we tested the performance of the four different model variants described above by calculating the log-transformed densities of the species in the previous years at four spatial scales. To do so, we applied spatial smoothing, using the exponentially decaying weighting function $e^{-d/r}$, where d is the pairwise distance between plots in km and r models the spatial scale of interactions.

HMSC uses Markov Chain Monte Carlo (MCMC) sampling to estimate the model parameters. In this method, the goal is to estimate the posterior distribution of the parameters given the observed data. MCMC sampling is used to explore and approximate this posterior distribution.

Subsequently, to determine the significance of inter-specific density dependence at the different spatial scales, we used a five-fold cross validation technique, comparing model predictions to observed data, to evaluate predictive- and explanatory power of the different model variants. To estimate the contribution of the remaining variables to the explained variance, we performed a variance partitioning for the model variant which excluded species interactions. We also estimated the percentage of unexplained variance.

Paper II

For the analyses performed in paper II and III, we developed a multivariate Poisson log-normal model which we applied to the time-series data of each community. Our approach builds on the theoretical framework developed by Engen & Lande (1996); Engen *et al.* (2002); Lande, Engen & Saether (2003); Engen (2007) and Engen, Grøtan & Sæther (2011), 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. Thus, our model assumes that the observed species abundances follow a Poisson distribution, while the true, underlying abundances are a realization from a normal distribution on the log-scale.

The PLND, first described by Grundy (1951), has been widely used for ecological study since its first application by Bulmer (1974) (see e.g., Connolly & Dornelas 2011; Grøtan *et al.* 2012; Sæther, Engen & Grøtan 2013), and contains valuable information on a communities' species diversity. For instance, the variance of this distribution acts as an inverse measure of evenness (Sæther, Engen & Grøtan 2013). More specifically, 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. In addition, the true underlying number of species of the community can be estimated from the probability density function of the distribution (Grøtan, Engen & Grøtan 2022). This is particularly valuable since accurately estimating species richness is notoriously difficult in natural communities (O'Hara 2005).

Previous studies have fitted the bivariate Poisson log-normal distribution to all pairs of samples to study community similarity (e.g., Engen, Grøtan & Sæther 2011; Grøtan *et al.* 2012; Grøtan *et al.* 2014) and to decompose the variance of the log-normal species abundance distribution (e.g., Engen *et al.* 2002; Engen, Aagaard & Bongard 2011). However, such an approach treats each pair of samples as being 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, σ^2, the correlation function of relative species abundances at different time-lags, as well as the community richness, *S*. This approach allowed us to take into account autocorrelations and trends in the data. Additionally, estimates may be assumed to become stabilized because information is drawn from multiple data-points in time.

More specifically, we let the vector of the log abundances of species *i* across all years, $\log(\boldsymbol{\lambda}_i)$, 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):

$$\log(\boldsymbol{\lambda}_i) \sim \mathrm{MVN}(\boldsymbol{\mu}, \Sigma). \tag{4}$$

Herein, we model the yearly mean log abundances μ_t as being dependent upon a community mean abundance across years (related to the general habitat quality of the community), potential trends arising from long-term changes in climatic conditions, as well as a variance influenced by common stochasticity acting equally on all species.

The community is further defined by the variance-covariance matrix, with the community variance σ^2 as its diagonal elements, and $\sigma^2 \times \rho_t$, where ρ_t is the correlation at time difference *t,* as its off-diagonal elements. We assume the function of autocorrelation in the time-series to decay exponentially.

We account for unobserved species by augmenting the data with multiple "species" with 0 observations across all years and use a zero-inflated model (see e.g., Royle, Dorazio & Link 2007; Zuur *et al.* 2009; Kéry & Royle 2020) to facilitate the process of estimating the true number of species in the community.

Thus, we model the counts (including the augmented data), *C,* for a given species (*i*) in a given year (*t*) as:

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

i.e. we let $C_{i,t}$ be a realization of the Poisson distribution with expectation $\lambda_{i,t}$ (see eqn. 4). a_i is a realization from a Bernouilli distribution with a probability π of being 1. Species richness, S, can be estimated as the sum of the discrete latent variables a_i.

We implemented our model using MCMC computation to find the joint posterior distribution of the parameters. Subsequently, we ran intercept-only models as well as linear and 2nd order polynomial models for each sample of the obtained (thinned) posterior distribution for all plots as well as separately for the plots of each of the two habitat types. We related 1) the estimates of species richness (*S*) and σ^2 to each other and 2) *S*, as well as the residuals of σ^2 after accounting for *S* to density (i.e., territories per area) and community biomass (i.e., bird biomass per area), as well as to latitude and Net Primary Productivity (NPP). We subsequently performed cross-validation to rank the model alternatives.

Paper III

The analyses in paper III build on the same multivariate Poisson log-normal model developed in paper II. In this paper, we perform a variance decomposition of σ^2, the total variance of the PLND. Our approach in this paper is a phenomenological model based on the theoretical framework developed by Engen & Lande (1996); Engen *et al.* (2002); Lande, Engen & Saether (2003); Engen (2007) and Engen, Grøtan & Sæther (2011), who showed that analyzing the decay in correlation in the species abundance distributions of a community over time (governed by the strength of density regulation) allows for a partitioning of the variance in the relative log abundances of the community into different components. Phenomenological models aim to describe and explain observable phenomena based on empirical data, without explicitly incorporating all underlying mechanisms in detail. In this case, the variance decomposition model allowed for the quantification of the relative contributions of ecological heterogeneity (σ^2_{heter}, i.e., differences in species' growth rates and thus log carrying capacities) as well as species-specific- (σ^2_{spec}) and common stochasticity (σ^2_{common}) to the overall community variance, without explicitly modeling the processes driving those variations.

We let the population fluctuations of the log abundances $X_1, X_2, \ldots, X_i$ of species i in the community (i.e., the species assembly at a given time *t* in a plot p) be described by the following discrete-time first-order autoregressive model:

$$X_{i,t+1} = r_i + \phi \times X_{i,t} + \varepsilon_{i,t} + E_t, \tag{6}$$

Herein, r_i are the species-specific, density-independent intrinsic growth rates. ϕ is the autocorrelation in log-abundance. $\varepsilon_{i,t}$ captures species-specific stochasticity, and E_t denotes common stochasticity, i.e., those events which affect all species of the community (including common environmental effects and certain types of competition). r_i, $\varepsilon_{i,t}$ and E_t are modelled as draws from normal distributions with mean $\bar{r}$ and 0, respectively, as well as variances σ_r^2, σ_s^2 and σ_c^2.

Based on the work by Engen et al. (2011), additionally defining a variance component attributed to the common stochasticity and adapted to a discrete-time process, the variance components σ_{heter}^2, σ_{spec}^2 and σ_{common}^2 can be found using the estimated parameters of eqn. 6. as follows:

$$\sigma_{heter}^2 = \frac{\sigma_r^2}{(1-\phi)^2} \tag{7}$$

$$\sigma_{spec}^2 = \frac{\sigma_s^2}{1-\phi^2} \tag{8}$$

$$\sigma_{common}^2 = \frac{\sigma_c^2}{1-\phi^2} \tag{9}$$

The model definition developed in paper III differs slightly from that in paper II in that we additionally accounted for autocorrelation in the annual deviations from the community mean log-abundance across all years. Such an autocorrelation may arise in populations returning to their carrying capacity after a disturbance. As mentioned, we also adapted the variance decomposition approach to a discrete-time process instead of a continuous one. This specification is important if density-dependence is strongly negative. In such a case, a continuous model specification would not be able to accurately capture the strong and abrupt population declines that would follow a over-shooting beyond the species' carrying capacity. In practice, for our data set, the change from continous- to discrete-time specification did not affect our results, but for species such as birds with discrete-time population growth, we considered this a more correct model definition.

We again implemented the model using MCMC computation to find the joint posterior distribution of the parameters. Subsequently, we related the different variance components to each other using linear regression on each sample of the (thinned) posterior distribution, evaluating statistical significance through cross-validation. We also investigated potential between-habitat differences in the proportion of variance explained by the three components by extracting the plot means of the three proportions for all iterations of the posterior distribution. We did these analyses for all plots across all habitats, as well as for the plots in each of the two habitat types (open and forest) separately. Further, we performed a Dirichlet regression (a multivariate generalization of beta regression) to predict changes in the three components of variance across species richness.

Main Results and Discussion

This thesis investigated the drivers of temperate bird community abundances in time and space, and thus, the findings of our study contribute to our understanding of the mechanisms underlying community assembly and highlight the complex interplay between deterministic and stochastic processes in shaping ecological communities. In the following, I will present a summary of the main results and discussions of the three papers of my thesis.

Paper I

This study was the first to apply the time-series implementation of Hierarchical Modeling of Species Communities (HMSC), modeling interspecific density dependence in three different ways. In this paper, we studied the relative importance of intra- and interspecific density dependence and environmental effects on the composition of temperate bird communities. We found intra-specific density dependence to be of great importance for community composition locally. The influence of intraspecific density dependence rapidly decreased with increasing spatial scale. Consequently, local population dynamics were largely unaffected by conspecifics at larger spatial scales. Environmental variables, such as temperature and precipitation, showed only a comparably small influence on the community dynamics. We did not find a strong structuring effect of interspecific interactions on the bird community, as including interspecific density dependence to the different model variants did not improve explanatory power nor predictive power at any spatial scale.

Using simulations, we verified that interspecies interactions should be detectable in our data, if present. A low signature of inter-species interactions supports the theory of stable coexistence, in which competitive exclusions can be expected to have already taken place (see e.g., Brown & Wilson 1956; Lack 1971; Connell 1980) or as an ongoing process confining each species to their current realized niches (e.g., Dhondt 2012; Tuck *et al.* 2018), leading to the contemporary species assembly in which intraspecific competition dominates over interspecific competition (e.g., MacArthur & Levins 1967; Chesson 2000; Barabás, J. Michalska-Smith & Allesina 2016). If, for instance, interspecific interactions primarily influence species' carrying capacities, and the species are currently fluctuating around these, we would not be able to detect the interactions that in the past led to the current community composition from the time-series data. Our findings are in accordance with this theory of niche differentiation, as well as recent studies supporting it (Adler *et al.* 2018; Barraquand *et al.* 2018; Tuck *et al.* 2018).

It is important to note that our results do not imply the absence or insignificance of interspecific interactions in bird communities. Rather, it is a question of the scale at which these interactions occur. Interactions between bird species are known to be of importance at the individual level (e.g., Källander 1981; Robb *et al.* 2008; Francis *et al.* 2018). However, they might not have a significant impact on the species' abundance fluctuations at the community level. Similarly, variables such as temperature and precipitation that might have a strong effect within single plots can appear to be less important as the focus is moved to a more general picture, as done here. Also, the temporal random effect, caused by environmental stochasticity, explained more of the total variation compared to the fixed environmental effects. This indicates that other environmental factors than those included in our model have an additional effect on the dynamics of the species. The random plot effect constituted a relatively prominent proportion of the variation even at the local scale, indicating permanent variation in habitat suitability among plots.

We conclude that it is advisable to conduct model selection prior to including interspecific interactions into community models, in terms of developing efficient models while avoiding overparametrization. At the same time, heterogeneity in the dynamics of single species, especially density dependence, is important to include to obtain a realistic understanding of community changes over time occurring at different spatial scales.

Paper II

In paper II, we investigated the relationship between community dynamics and productivity in two different habitat types (open and forest). We did not find strong support for any relationship between species richness and the evenness in the distribution of abundance of species in the community. Further, richness and evenness showed distinct responses to various measures of productivity: While richness was clearly related (but not in a simple, linear way, discussed below) to productivity, we did not see any evidence for a bottom-up regulation of evenness.

Several previous studies have investigated the richness-evenness relationship in birds. Later investigations consistently report a negative relation for this taxa (e.g., Pautasso & Gaston 2005; Bock, Jones & Bock 2007; Sæther, Engen & Grøtan 2013; Berduc, Lorenzón & Beltzer 2015). Similarly, our study found a slight positive relationship between species richness and the variance in species abundance distribution, indicating a slightly negative relationship between species richness and evenness. However, our simulation study revealed that such a relationship can arise even in the absence of an actual relationship between variance and richness, highlighting the challenge of producing a measure of evenness that is fully independent of richness (Jost 2010). Therefore, we strongly encourage the use of simulations to verify results also in future studies. Also, our findings indicate that richness does not reflect evenness in a simple way. There have been many calls for treating richness and evenness as distinct measures of species diversity (e.g., Whittaker 1965; Magurran 1988; Weiher & Keddy 1999), and our study suggests the same.

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, and we observed an increase in species richness with increasing levels of community biomass. However, richness increased with increasing density only in forest habitat types, but not in open habitats. 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 across habitats and in open habitat types, but no relationship in forest habitats. This may indicate richness to be more independent of productivity levels in more heterogeneous habitats, for example if these can provide more opportunities for niche division.

Relative evenness (i.e., evenness after correcting for the slight dependency with richness, σ_{res}^2) was not influenced by any of the aspects of total abundance (number of territories or total biomass) in the communities, nor by NPP. Thus, we did not find any support here for a bottom-up regulation of evenness in the studied bird communities. There are many other factors that could potentially influence evenness, for instance the scale of the study. The observed patterns of evenness may vary depending on the spatial extent and resolution of the data. Additionally, the interplay between bottom-up (resource availability) and top-down (predator-prey interactions) regulation might be a potentially important factor shaping evenness. Further research is needed to better understand the specific mechanisms underlying the observed patterns of evenness and to explore the potential interplay of various ecological factors.

Paper III

In paper III, we conducted a variance decomposition analysis to assess the contributions of ecological heterogeneity as well as species-specific and common stochasticity to the overall community variance. Heterogeneity among species, reflecting differences in growth rates and log carrying capacities, was found to explained on average ~93 % of the total variance in the studied communities. Forest habitats showed a larger proportion of variance explained by heterogeneity compared to open habitats [open: ~92 %, forest: ~95 %]. Moreover, the proportion of variance explained by species-specific as well as common stochasticity was reduced in forest- compared to in open habitat types. The proportion of variance explained by species-specific stochasticity increased with increasing species richness.

High ecological heterogeneity among species leads to a low rate of decay in community correlation over time, indicative of low temporal turnover in species relative abundances (McGill et al. 2015). Thus, the observed community structure may be indicative of a state of stable coexistence (although it is important to note that changes can disrupt this stability and lead to shifts in species composition and higher rates of temporal turnover). The observed stability in community structure may arise by different mechanisms, such as for instance density regulation (e.g., May 1974; Chesson 2000), past competition (e.g., Rosenzweig 1987; Rosenzweig 1991), or niche differentiation (e.g., Hutchinson 1957; Schoener 1974). The strong contribution of σ^2_{heter} to the total variance observed here indicate that the species' abundance fluctuations are bounded around their respective carrying capacities, suggesting strong density regulation, which is in line with our findings from paper I.

The reduction of levels of and proportion of variance explained by both species-specific- and common noise in forest habitats may be due to a variety of different factors. For instance, forest habitats may provide a more stable and predictable environment (e.g., Whittaker 1970; Leibold & Chase 2017). Also, greater availability of resources and available shelters due to a richer microclimatic variation in forest habitats may also buffer against the effects of stochasticity (e.g., MacArthur & MacArthur 1961; Pearsons, Li & Lamberti 1992). We observed that the between-habitat difference was larger for species-specific than for common noise. Thus, forest habitats may offer only some degree of protection against the effects of common stochastic events such as e.g. extreme environmental conditions.

Additionally, we observed an increase in the proportion of variance explained by species-specific stochasticity with increasing estimated number of species. There was a corresponding decrease in the proportion of variance explained by heterogeneity. This relationship remained significant even after accounting for the richness-area relationship. The observed pattern might arise from superior species being able to outcompete others in environments that experience less disturbance (e.g., Grime 1973; Huston & Huston 1994). Additionally, a larger influence of stochasticity may promote richness for instance through temporal openings of new niches (e.g., Chase & Leibold 2009; Leibold & Chase 2017). Alternatively, niche size of each species might decrease with increasing richness (e.g., Holt, Grover & Tilman 1994; Tilman 1994), potentially increasing the vulnerability of each species to stochasticity.

While the proportion of variance explained by species-specific noise increased with richness, the proportion explained by common noise was unaffected by richness. It has been proposed that species richness might increase stability by decreasing synchrony, because higher richness increases the chances that some of the species will respond individually to environmental factors (McCann 2000; Valencia *et al.* 2020). Assuming a larger proportion of variance explained by common noise to be suggestive of synchrony, here, we did not see any indication of a relationship between synchrony and species richness. However, we did observe an increase in species richness with increasing proportion of variance explained by species-specific noise. This is in line with previous research which stresses the importance of between-species differences in their responses to the environment for the diversity-stability relationship (e.g., De Mazancourt et al. 2013; Loreau & De Mazancourt 2013). The relationship between richness, stability and synchrony is intricate (Valencia *et al.* 2020), and more investigation is necessary.

Summary and Future Prospects

Sustainable management decisions and successful conservation efforts need to be based on the solid foundation of knowledge about the structuring forces underlying observed patterns in nature. Especially in a world of ever-increasing anthropogenic demands on natural resources and space, combined with the tangible threat of climate change, attempting to answer the long-standing core questions within the field of community ecology is as relevant and urgent today as ever before. For instance, we still do not fully understand the factors which determine species diversity and the distribution of species within ecosystems, or which mechanisms are driving the observed patterns of species coexistence and what the role of biotic and abiotic factors are in shaping community structure. Furthermore, understanding how communities respond to different biotic and abiotic factors, such as interactions between species or environmental changes and disturbances, is crucial for the protection and management of ecosystems.

Throughout the thesis, intra-specific density dependence and ecological heterogeneity emerged as important factors shaping community dynamics, while the signature of inter-specific density dependence on community abundance data was small. High ecological heterogeneity indicates low temporal turnover in relative abundances of species, which is associated with community stability. Additionally, the observed pattern of weak inter- but strong intra-specific density dependence is in line with expectations from the theory of stable coexistence. Environmental variables and stochasticity played a comparatively small role, highlighting the importance of deterministic processes in shaping European bird community structure. We also found that increased habitat complexity was related to decreased levels and impact of species-specific and common stochasticity, indicating buffering effects and/or stronger niche differentiation in forests. Additionally, we found species diversity to be linked to net primary productivity and habitat complexity. The two components of species diversity—richness and evenness—showed differentiated responses to productivity gradients: While richness was clearly related to (but not fully explained by) productivity, we did not see any evidence for a bottom-up regulation of evenness. Stochasticity and/or the degree of between-species differences in their responses to stochasticity additionally seems to be involved in determining species richness.

In this thesis, I have attempted to address some of community ecologies' most long-standing questions by applying and developing multivariate statistical tools. The work done here is thus also an attempt to widen the horizon in terms of the use of statistical methodology within the field of community ecology. The investigations performed in all three papers were based on extensive time-series count data distributed along a latitudinal gradient. As such, our analyses provided an important temporal and spatial dimension to central community ecology questions, contributing to a broader knowledge of community ecology and providing valuable insights that may be used in further research as well as for sustainable conservation and management strategies in temperate bird habitats.

A natural next step in the work that we have started on here would be to extend our multivariate Poisson log-normal model to also include a spatial aspect. This extension would greatly increase computational effort, but such an approach would enable us to additionally utilize the information stored in the potential spatial autocorrelation between the plots in the parameter estimation process. Additionally, this extension could allow us to take into account possible over-dispersion and/or estimate demographic stochasticity.

In addition, the simulations performed in paper II indicate that common metrics of evenness will tend to produce some relationship with richness even when there actually is none. Thus, it would be interesting to further explore the potential use of the variance of the Poisson log-normal distribution as an inverse measure of evenness which is possibly less interrelated with richness. Depending on availability of data, one could thus fit our multivariate PLND also to communities of other taxa and/or other locations to similarly check the produced patterns against simulations.

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"But ask the animals, and they will teach you, or the birds in the sky, and they will tell you;
or speak to the earth, and it will teach you, or let the fish in the sea inform you.
Which of all these does not know that the hand of the Lord has done this?
In His hand is the life of every creature and the breath of all mankind."
~ Job 12:7-10

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Paper I

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ARTICLE

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Effects of density, species interactions, and environmental stochasticity on the dynamics of British bird communities

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Abstract

Our knowledge of the factors affecting species abundances is mainly based on time-series analyses of a few well-studied species at single or few localities, but we know little about whether results from such analyses can be extrapolated to the community level. We apply a joint species distribution model to long-term time-series data on British bird communities to examine the relative contribution of intra- and interspecific density dependence at different spatial scales, as well as the influence of environmental stochasticity, to spatiotemporal interspecific variation in abundance. Intraspecific density dependence has the major structuring effect on these bird communities. In addition, environmental fluctuations affect spatiotemporal differences in abundance. In contrast, species interactions had a minor impact on variation in abundance. Thus, important drivers of single-species dynamics are also strongly affecting dynamics of communities in time and space.

KEYWORDS

community dynamics, density dependence, environmental stochasticity, joint species distribution model, multi-species, spatiotemporal, species interactions, time-series

INTRODUCTION

While single-species dynamics are reasonably well understood, much less is known about the potential importance of various deterministic and stochastic processes on the community level (e.g., Engelhardt et al., 2020; Kinzey & Punt, 2009).

From time-series studies of single, or few, species, we know that density dependence, i.e., a negative effect of current, or previous year's population densities on the population growth rate, is an important process affecting population dynamics (e.g., Lande et al., 2003; Royama, 1992). This can occur, e.g., through intraspecific competition for limited resources (e.g., Hansen et al., 1999; Newton, 1998) or through interference competition that excludes individuals' access to space (e.g., Denac, 2006; Moksnes, 2004). Brook and Bradshaw (2006) found that about 75% of 1198 invertebrate and vertebrate species, including birds, showed intraspecific density dependence in their per-capita growth rates. Intraspecific density dependence in birds has been found to vary in strength and form both between (Sæther et al., 2002) and within species (Sæther et al., 2008), influenced for example by species-specific life-history strategies such as generation time or by local adaptations within species to spatial

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variation in the biotic and abiotic environment (Sæther et al., 2002, 2005).

Interspecific competition is also a potentially important structuring force in natural communities (e.g., Cody et al., 1975; Elton, 1946; Gause, 1934; Hardin, 1960). Both intra- and interspecific interactions are fundamental to classical niche theory (Hutchinson, 1947, 1967, 1978), according to which stable coexistence of species is possible through resource partitioning (e.g., Lande et al., 2003; Mittelbach, 2012; Tilman, 1982). Interspecific density dependence, i.e., the effects of changes in one species' abundance on that of other species, is considered important in regulating species abundances (May et al., 1974; Rosenzweig, 1995) and ample experimental and observational quantification shows its importance also in birds (e.g., Alatalo et al., 1987; Dhondt, 2012; Gamelon et al., 2019). Central to coexistence theory is that density dependence within species must be stronger than that between species (Chesson, 2000) and recently, Adler et al. (2018) found evidence for this pattern in their review of plant studies.

Population fluctuations are additionally influenced by environmental stochasticity, i.e., between-year variation in populations' expected survival and fecundity caused by random variation in the environment, such as, e.g., weather variables, pollution, or habitat loss, which affects all, or groups of, individuals exposed to it similarly (Lande, 1993; Lande et al., 2003). Environmental stochasticity tends to reduce the long-run population growth rate (Lande et al., 2003; Lewontin & Cohen, 1969) and has been shown to strongly affect many species (Dobinson & Richards, 1964; Grant, 1986; Grøtan et al., 2009; Sæther et al., 2016).

Demographic stochasticity, i.e., within-year variations between individuals in their survival and fecundity (Engen et al., 1998; Lande et al., 2003; MacArthur & Wilson, 1967) is also widely accepted as being an important process in population dynamics. It is known to have the strongest influence at low population sizes, because variation in individual fitness lowers the long-term population growth rate, increasing risk of extinction (e.g., Lande, 1993; Melbourne & Hastings, 2008). Demographic stochasticity is the major form of stochasticity in neutral theories of community dynamics (Hubbell, 2001).

The scale, both in time and space, at which communities are observed, determines what patterns are perceived (Allen & Hoekstra, 1991; Levin, 1992). Species can perform differently in different environments (e.g., Levine & Rees, 2002; Wiens, 1989), so that their growth rates vary across space, and two species may thus co-exist in areas that are not optimal for one/both of them, while they might be competitively exclusive in more favorable environments. Additionally, movement can greatly influence occurrence patterns (Martin et al., 2017; Wiens, 1989). In other words, interspecific interactions can affect occurrence patterns not only locally, but on a larger spatial scale as well (Araújo & Rozenfeld, 2014; Gotelli et al., 2010). Also, temporal variation in the environment allows coexistence of species even with exactly overlapping niches, due to temporal openings of local niches (Chesson, 2000; Hutchinson, 1951). To obtain a complete picture of the species community, studies should be conducted for long time periods and at large spatial scales (Ives et al., 2003; Magurran, 2007; Magurran et al., 2010), ideally retaining the species-level information.

The aim of this study was to increase our understanding of the drivers of community changes over time occurring at different spatial scales using unique large-scale, long-term time-series data existing on British bird communities. We use joint species distribution models (JSDMs) with latent variable structures, taking into account both abiotic and biotic processes in an integrated way (Warton et al., 2015) to examine the relative contribution of intra- and interspecific density dependence at different spatial scales, as well as the influence of environmental stochasticity, to spatiotemporal variation in abundance.

Recent studies have investigated various community drivers at different spatial scales (Karp et al., 2018, Frishkoff et al., 2019) based on information on the individual species of the community. However, studies based on time-series data are still rare (but see Hendershot et al., 2020).

MATERIALS AND METHODS

Common Bird Census data

We utilized estimates of territories 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). The CBC was a program monitoring populations of common bird species in farmland and woodland plots using territory mapping from 1962 to 2000 (Marchant et al., 1990). The CBC was replaced by the BBS (using line transects) in 2001, with a period of overlap where the established plots were continued, to ensure compatibility of the two methods (Freeman et al., 2007). We included only data from 1962 to 2002 (i.e., all data obtained from territory mapping) and used plots monitored continuously for ≥10 years (a few plots had two such stretches of observations; in which case, we included both), resulting in community time series of 10–36 years between 1965 and 2002, from a total of 121 plots (68 farmland and 53 woodland plots) distributed across large parts of the UK (excluding Northern

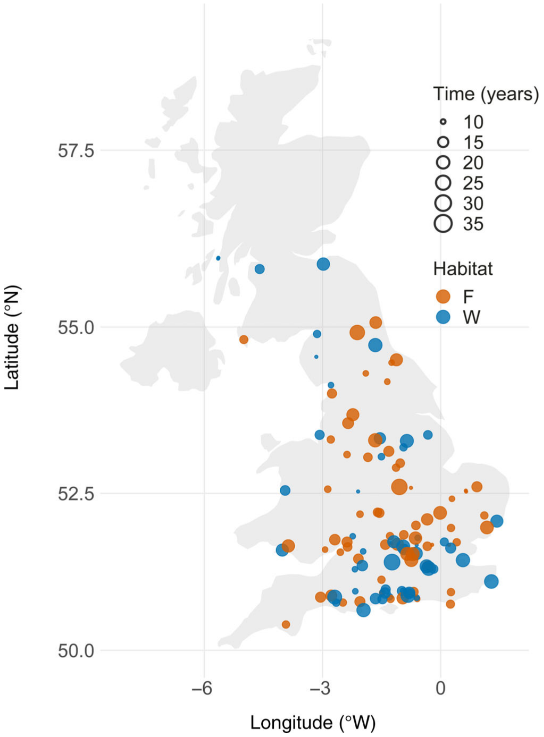

FIGURE 1 Distribution of farmland (F, orange) and woodland (W, blue) plots monitored by the British Trust for Ornithology (BTO; Common Bird Census [CBC] and Breeding Bird Survey [BBS]). Time-series length (in years) is indicated by circle size, with a minimum of 10 consecutive years in the period 1962–2002 ($n = 121$ plots)

Ireland), see Figure 1. The mean size in square kilometers for farmland plots was 0.8 (minimum, 0.19; maximum, 3.13) and 0.25 for woodland plots (minimum, 0.11; maximum, 0.6). We excluded species ecologically linked to aquatic communities as well as species observed in <30% of the plots. While one of the advantages of joint species distribution modeling is that parameter estimates for rare species are facilitated by information on responses of more common species (Ovaskainen & Abrego, 2020; Ovaskainen & Soininen, 2011), we nevertheless adopted a conservative approach by ensuring a minimum quality of the input data. For the full species list, see Appendix S1: Table S1.

Environmental data

The effects of environmental variables on population abundances of birds are often complex, including direct, indirect and time-lagged effects (Pearce-Higgins et al., 2015; Sæther & Engen, 2010). We applied a sliding time-window approach (van de Pol et al., 2016) to detect the critical time window during which two key environmental factors, temperature and precipitation, influence the abundance of each species the most. We extracted monthly mean temperature (°C) and precipitation sum (mm) for each plot from the corresponding 5-km^2 resolution climate data grid obtained from the Met Office UKCP09 databases (13.09.2017; MetOffice, 2017) for the duration of the plot-specific sampling period (>10 years, ranging from 1965 to 2002). There were only 11 out of our 121 plots for which the climate data from the same grid was shared with one (and in one single case, two) other plot(s). To identify the start and end of the time windows of the species-specific variables that best predicted the observed population dynamics, we followed the regression based sliding time-window approach by van de Pol et al. (2016). We transformed the estimates of territories n into an estimate of log-transformed density y (number of pairs of individuals per unit area) because of the well-known influence of area on bird abundances (e.g., Ambuel & Temple, 1983; van Dorp & Opdam, 1987), by $y = \log[(n+1)/A]$, where A is the area of the plot, and we added 1 to n to assure positive values. For each species, we evaluated the best combination of time windows of the two environmental covariates based on the Akaike information criterion (AIC) value of the baseline model (a simple first-order autoregressive model of the log population densities with plot as random effect) compared to a model including the aggregate statistics of a certain time-window (either of one, both, or none of the covariates). We allowed for the selection of a window spanning up to 12 months prior to June at year t, the last month of the census (hence, the longest possible time-window tested for extended from June at time $t-1$ to May at time t). The best combination sometimes included only one, or even none, of the covariates; see Sandal et al. (2022) for the three top-ranking combinations for each species.

Hierarchical joint species distribution modeling

We analyzed the data with hierarchical modeling of species communities (HMSC), a JSDM, using the implementation for time-series data by Ovaskainen et al. (2017). This approach utilizes first-order multivariate autoregressive [MAR(1)] models, a tool used to infer strengths of both between- and within-species interactions (Ives et al., 2003; Novak et al., 2016; Wootton & Emmerson, 2005). MAR (1) models can be used as relatively simple approximations to complex natural systems, and essentially represent multispecies Gompertz dynamics (Certain et al., 2018; Ives et al., 2003). We followed the approach by Ovaskainen et al. (2017), using three different methods of including species interactions, compared to a variant excluding any interspecific interactions. See Appendix S2 for a detailed outline of the model structure. Common for all model variants, the response variable was the vector of log-transformed species densities. We scaled these so that each species had zero mean and unit variance to make the species comparable among each other. Subsequently, we added plot-specific constants (the same for all species) so that $\sum_{it} y_{ipt} = 0$, i.e., all plots had the same average summed species density (y being the standardized, log-transformed densities used as the response variable in the models). This step accounted for unknown variation in general habitat quality and sampling effort at the community level, while species-specific variations are accounted for by the random effect described in eq. 1 below (see Appendix S3 for details on the linear transformations applied to the data before model fitting).

The linear predictor of the standardized log-transformed density of species i at plot p in year t (L_{ipt}) was defined as

$$L_{ipt} = L_{ipt}^{\mathrm{F}} + L_{ipt}^{\mathrm{R}} + e_{ipt} \qquad (1)$$

where L_{ipt}^{F} includes the fixed effects, L_{ipt}^{R} the random effects, and e_{ipt} the residual, which we assumed to be normally distributed for the log-transformed densities. The fixed part was further decomposed as $L_{ipt}^{\mathrm{F}} = L_{ipt}^{\mathrm{E}} + L_{ipt}^{\mathrm{A}}$, where L_{ipt}^{E} modeled the environmental effects (by the environmental covariates included in the model) and L_{ipt}^{A} the species interactions (by the previous years' densities, see the following paragraphs).

As environmental covariates, we used the two species-specific climatic variables identified before. Habitat type (farmland and woodland) was included as a factor, and log area of the plot was included as a continuous covariate, to account for possible nonlinear effects of plot area. To account for within-species density dependence, we included the density of the focal species in the previous year as a species-specific covariate. We calculated the density of the species in the previous year at four different spatial scales, as explained in the section titled *Spatial scale of intraspecific density dependence and interspecific interactions*.

All continuous covariates were mean centered and scaled to unit variance to make them compatible with the default priors of HMSC. To account for unmeasured covariates that create permanent spatial variation among the plots (i.e., variation in habitat quality among sites), we included plot ($n = 121$) as a spatially explicit random effect using latent variables with exponentially decaying spatial covariance structure (Ovaskainen et al., 2016). See Appendix S4: Table S1 for the estimates of the spatial scaling of the spatial random effect. Additionally, to be able to quantify the magnitude of temporal variability in the community abundance through time due to environmental conditions affecting all species simultaneously, we included year ($n = 38$) as a temporally explicit random effect, also with a exponentially decaying covariance structure (to account for the distance in time between sampling events).

We modeled species interactions as

$$L_{ipt}^{\mathrm{A}} = \sum_{j=1}^{m} \alpha_{ij} y_{jpt-1} \qquad (2)$$

where m is the number of species, α_{ij} models the effect of species j on species i, and y_{jpt-1} is the standardized, log-transformed density of species j at plot p the previous year. The interaction term α_{ij} was specified differently for the different variants of the model as follows (see Appendix S2 and Ovaskainen et al., 2017 for more details).

Model variant M1: No interspecific interactions

Only diagonal elements α_{ii} that model intraspecific density dependence were estimated, whereas the effects of interspecific interactions were excluded by fixing $\alpha_{ij} = 0$ for $i \neq j$.

Model variant M2: Full interactions

We included as predictors the densities of all the species in the previous year, thus estimating a full matrix of species-to-species interaction coefficients.

Model variant M3: Sparse interactions

We assigned for interaction coefficients α_{ij} a multiplicative prior in which the first factor modeled whether the interaction either was zero (with prior probability 0.9) or non-zero (with prior probability 0.1), and the second factor had the same normally distributed prior as in model variant M2.

Model variant M4: Community-level drivers

We modeled interspecific competition α_{ij} as

$$\alpha_{ij} = \sum_{k=1}^{n_d} q_{i,k} w_{k,j} + \delta_{ij} \iota_i. \qquad (3)$$

Herein, species are assumed to contribute to one or more of n_d "community-level drivers", defined as linear combinations of species densities, ecologically corresponding to e.g., total community biomass. As in Ovaskainen et al. (2017), we estimated both the contribution (w) of each species j to each driver k, as well as the influence of each driver to each species $q_{i,k}$. Additional effects of intra-specific interactions ι_i (beyond those captured by the community-level drivers) are added to the interaction matrix via the Kronecker's delta δ_{ij}, which is 1 for δ_{ii}, and otherwise 0. We assumed the prior of Ovaskainen et al. (2017) that increases shrinkage with the index of the driver and fixed the number of drivers to two.

We acknowledge that such a model would be better if implemented as a state-space model, i.e., accounting for a discrepancy between true and observed population sizes. In its current form, this is not fully possible in HMSC. Observation error is accounted for in the response, but not in the predictor, and it would be better to separately account for the process and observation error. However, our simulations confirm that even the current model does detect species interactions, if present (Appendix S7: Table S1 and Figure S1).

Spatial scale of intraspecific density dependence and interspecific interactions

We tested the performance of the four different model variants by calculating the log-transformed densities of the species in the previous years at four spatial scales. Thus we applied spatial smoothing, using the exponentially decaying weighting function $e^{-d/r}$, where d is the pairwise distance between plots in kilometers and r models the spatial scale of interactions. We compared four contrasting spatial scales called henceforth local (denoted by L) scale ($r_0 \rightarrow 0$, thus applying no smoothing), proximal (P) scale ($r_1 = 18$ km equaling the average distance to the nearest plot), average (A) scale ($r_2 = 204$ km equaling the average distance between plots), and regional (R) scale ($r_3 = 711$ km equaling the maximum distance between plots). Note that, in addition to modeling the influence of large-range interactions, spatial smoothing space may increase the predictive power of the models by reducing noise in the predictor.

Model fitting

The combination of four model variants and four spatial scales results in 16 models. We denote these by MA-B, where A is the model variant and B is the spatial scale, so that, e.g., M3-R is the model variant 3 (sparse interaction), with the species densities in the previous year measured at the regional scale. We fitted the 16 models used the R package *Hmsc-R* (Tikhonov et al., 2020) assuming the default prior distributions (for details, see Ovaskainen & Abrego, 2020: Chapter 8). We sampled four MCMC chains with 37,500 iterations each, discarded the first one-third (12,500 iterations) as burn-in, and thinned the remaining by thin = 100 to yield 250 MCMC samples per chain and thus 1000 samples in total. We evaluated MCMC convergence visually by checking posterior trace plots (see Appendix S6: Figure S1) as well as quantitatively by examining the potential scale reduction factors of the model parameters (see Appendix S6: Figure S2; Tikhonov et al., 2020).

Deriving ecological inferences from the fitted models

To examine the predictive power of the different model variants at the different spatial scales, we applied for each of the fitted 16 model variants a five-fold cross-validation strategy, a technique that ensures the independence of model predictions from the data used to evaluate the accuracy of the predictions (Refaeilzadeh et al., 2009). We randomly split the years into five equal folds and fitted each model variant five times, each time masking the observations from one of the folds, and then combining the predictions from different folds to yield predictions for the entire data. For each species and each plot, we measured the predictive power as the correlation between these predicted and the observed species densities. For some cases (i.e., a time series of a particular species in a given plot) the calculation of correlation was not meaningful because of lack of sufficient variation, e.g., due to the species being mostly absent from the plot. To account for this, cases where the observed values differed from the modal value of that case for <5 years were excluded from the calculation of predictive and explanatory power.

We averaged the correlations over the plots to obtain a mean correlation for each species, and we then averaged over the species to obtain a mean correlation for each of the 16 model variants. We successfully validated the ability of the cross-validation procedure to reveal the true structure of the interaction network with the help of simulated data (see Appendix S7 for details). We evaluated explanatory power by comparing the predictions from models fit with the full data (no years masked) to the observed data.

To estimate how much other variables than species interactions contributed to the explained variance, we utilized the function computeVariancePartitioning() from the *Hmsc* package (Tikhonov et al., 2020) to partition the explained variance of model variant M1 (i.e., without species interactions) among the fixed and random effects; see Appendix S5 for details. To evaluate additionally the percentage of unexplained variance, we first estimated the amount of explained variance for each species as the total variance (measured in the log-transformed data, before normalization) multiplied by the mean R^2 value of the model, which in *Hmsc* corresponds to the proportion of explained variance. We subsequently found the amount of unexplained variance as the total variance minus the amount of explained variance. To facilitate comparison in the variance decomposition among species, we then scaled the sum of both explained and unexplained variance to 1 for each species and calculated the mean values for the percentage of variance allocated to each variable. To express intraspecific density dependence in terms of the effect of previous years' log population densities on growth rate (rather than on the current log population density), we subtracted 1 from the model estimates of the effect of intraspecific density dependence. We used the ggplot2 package (Wickham, 2016) to visualize our results.

RESULTS

Evaluation of alternative models for species interactions

The explanatory and predictive power of the models decreased substantially with the spatial scale of intraspecific density dependence and interspecific interactions, with the local scale L providing the highest explanatory and predictive power (mean explanatory and predictive power ranging from L, 0.37 to R, 0.27 and from L, 0.33 to R, 0.07, respectively). Using the model without interactions (M1) as baseline for comparison, neither explanatory or predictive power increased substantially by including species interactions into our models (M2-4; Table 1) at any of the spatial scales (local [L], proximal [P], average [A], and regional [R]). If the bird communities were structured by species interactions to a large degree, one would expect M1 to have a low explanatory power, while the other model variants would perform better in comparison. At the local and proximal scale, models M2, M3, and M4 had a somewhat higher explanatory power than the simplest model M1, because these models are more complex and provide a tighter fit. The predictive power for the respective models was slightly decreased, further indicating that the slight increase in explanatory power was due to a higher number of parameters included in these models. Appendix S7: Table S1 and Figure S1 distinctly show the expected increase in both explanatory and predictive power in M2–M4 compared to M1 for a simulated data set with clearly defined species interactions.

This pattern was retained also when examining the comparison of explanatory and predictive power of models M2–M4 to the baseline model M1-L at the level of individual species (Figure 2a,b). Especially for M2 we observed a somewhat increased explanatory power compared to M1 for most species, even at larger spatial scales of species interactions, but with a simultaneous decreased predictive power. For M3 and M4, locally, explanatory power was slightly better for most species, but not at any of the larger scales. Including species interactions did not improve the models' ability to predict the dynamics of any particular individual species, as M2-L, M3-L and M4-L did not give substantially better predictions than M1-L for any of the species (Figure 2b). The predictive power further decreased for all species as the local scale of species interactions was increased. Mean values of explanatory power and predictive power (Table 1) were similar between all model variants at the local and the proximal scale, but at the average, and especially at the regional scale, explanatory

TABLE 1 Explanatory and predictive power of the models M1–M4 at the four different spatial scales of species interactions

	Explanatory power				Predictive power			
Scale	**M1**	**M2**	**M3**	**M4**	**M1**	**M2**	**M3**	**M4**
L	0.366	0.392	0.370	0.369	0.336	0.320	0.334	0.333
P	0.346	0.382	0.351	0.352	0.293	0.275	0.288	0.293
A	0.275	0.367	0.297	0.226	0.111	0.114	0.104	0.095
R	0.267	0.365	0.280	0.168	0.078	0.048	0.064	0.065

Notes: Explanatory power is measured as the mean of the correlation for each species in each plot between the observed time-series and time-series predicted by the different models fit to the observed data. Predictive power is measures as the mean of the correlation for each species in each plot between the observed time-series and independently predicted time-series obtained by fivefold cross-validation. Scales are L (local scale), no spatial smoothing; P (proximal scale), average distance to the nearest neighboring plot (18 km); A (average scale), the average distance between plots (204 km); R (regional scale), maximum distance between plots (711 km).

power was higher than predictive power, indicating that these models might be overfitted.

In summary, we do not find a strong signal of interspecific interactions. Our simulations show that the modeling approach would be able to capture biologically significant interactions, if present, and we thus conclude that our results are not a statistical artifact.

Relative contributions of intraspecific density dependence and environment

For M1, we partitioned the variance among fixed and random effects, as well as unexplained variance (Table 2). M1 was able to explain on average between 63.6% and 70.8% of the variation in the species'

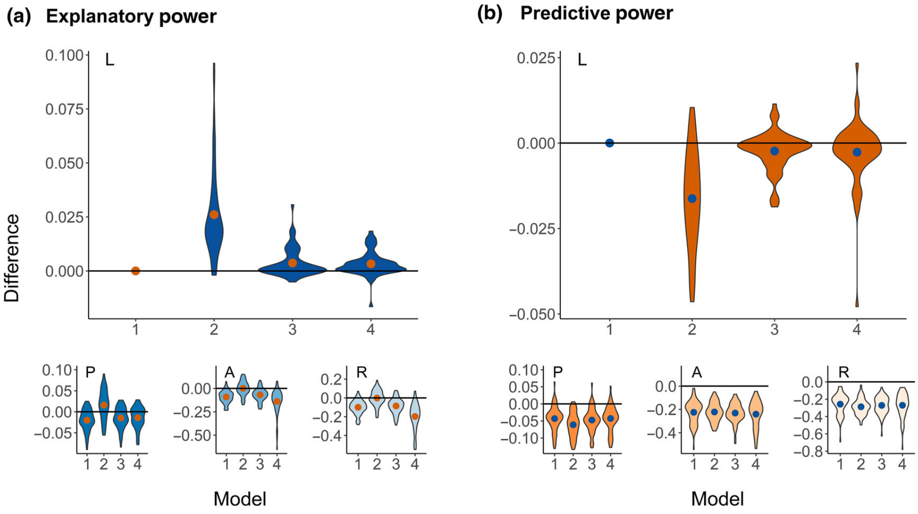

FIGURE 2 The difference for each species in (a) explanatory power and (b) predictive power between the focal model and the generally best model M1-L. The horizontal lines indicate a difference of zero. The four subpanels in each panel, L–R, show results at each of the four spatial scales (L, local; P, proximal [18 km]; A, average [204 km]; R, regional [711 km]; increasingly light color), for the four different models, so that L1 = (M1-L) − (M1-L) = 0, L2 = (M2-L) − (M1-L), L3 = (M3-L) − (M1-L), L4 = (M4-L) − (M1-L), P1 = (M1-P) − (M1-L), ..., R4 = (M4-R) − (M1-L). The mean difference is indicated by a dot. Values for M1-L are exactly zero, since they are being compared with self

TABLE 2 Average percentage of variance partitioned among fixed and random effects, as well as unexplained variance, for model 1 (no species interactions) at the four different spatial scales of species interactions

	Scale (%)			
Factor	**Local**	**Proximal**	**Average**	**Regional**
Fixed effects				
Density dependence	20.1	4.8	0.6	1.0
Habitat	1.2	1.6	2.7	1.9
Log area	1.4	4.9	5.5	4.3
Precipitation sum	0.3	0.2	0.2	0.1
Mean temperature	0.6	0.4	0.4	0.3
Random effects				
Plot	31.7	42.4	51.2	53.5
Year	15.5	14.3	4.0	2.6
Unexplained variance	29.2	31.4	35.4	36.3

Notes: Note that only density dependence is subject to the spatial smoothing. Local scale, no spatial smoothing; proximal scale, average distance to the nearest neighboring plot (18 km); average scale, the average distance between plots (204 km); regional scale, maximum distance between plots (711 km).

log-densities across the four spatial scales. Note that the proportion of explained variance was higher than the average explanatory power (0.37). This is because the measure of explained variance includes, e.g., the variation between plots, while such variance is not included in the within-plot correlations performed to measure explanatory power due to the normalization of the data. The partitioning revealed a strong, localized effect of intraspecific density dependence, as evidenced by a reduction from constituting 20.1% of the variance at the local scale to only 4.8% at the proximal scale. At an even larger average and regional scale, intraspecific density dependence explained only between 0.6% and 1%. The species-specific temperature and precipitation time-windows included into the model explained only a small proportion of the explained variation at the local scale. Habitat and log area constituted, relative to density dependence, a moderate amount of variation. Note that only density dependence was subject to spatial scaling, hence it is most meaningful to analyze the partitioning at the local scale. Random plot effects increased from L, 31.7% to R, 53.5%, while the random temporal effect decreased from L, 15.5% to R, 2.6%.

DISCUSSION

We studied the relative importance of intra- and interspecific density dependence and environmental effects on the composition of temperate bird communities. Intraspecific density dependence was of great importance locally (Table 2). The influence of intraspecific density dependence rapidly decreased with increasing spatial scale. Consequently, local population dynamics were largely unaffected by conspecifics at larger spatial scales. Environmental stochasticity, such as temperature and precipitation, showed only a comparably small influence on the community dynamics (Table 2), as will be discussed in more detail later. We did not find a strong structuring effect of interspecific interactions on the bird community, as including interspecific density dependence to the different model variants did not improve explanatory power nor predictive power at any spatial scale (Table 1 and Figure 2).

Inter- and intraspecific density dependence in the light of stable coexistence

Model performance was not enhanced by accounting for interspecific density dependence. Similarly, Mutshinda et al. (2009) did not find any strong signature of cross-correlations in species abundances in their comparative analyses of long-term studies of communities of moths, fishes, macrocrustaceans, birds, and rodents (data covering up to 40 years in time). In their review of studies in plants, Adler et al. (2018) report a weak influence of interspecific compared to intraspecific effects in the majority of cases.

Our simulations verified that interspecies interactions should be detectable in our data, if present (Appendix S7: Table S1 and Figure S1). Thus, the lack of an increase in model performance is not a statistical artifact and could be attributed either to (1) the nature of data collected in large-scale, long-term community ecology studies, (2) an actual low influence of species interactions on the contemporary community composition, or (3) a combination of the two. Naturally, the area of the plots sampled are limited, and there will be differences in species detectability as well as in between-observer repeatability (Buckland et al., 2011; O'Connor & Marchant, 1982; Williamson & Homes, 1964).

On the other hand, a low signature of interspecies interactions supports the theory of stable coexistence, in which competitive exclusions can be expected to have already taken place (see, e.g., Brown & Wilson, 1956; Connell, 1980; Lack, 1971) or as an ongoing process confining each species to their current realized niches (e.g., Dhondt, 2012; Tuck et al., 2018), leading to the contemporary species assembly in which intraspecific competition dominates over interspecific competition (e.g., Barabás et al., 2016; Chesson, 2000; MacArthur & Levins, 1967). If, for instance, interspecific interactions primarily influence species' carrying capacities, and the species are currently fluctuating around these, we would not be able to detect the interactions that in the past led to the current community composition from the time-series data. Our findings are in accordance with this theory of niche differentiation, as well as recent studies supporting it (Adler et al., 2018; Barraquand et al., 2018; Tuck et al., 2018): while including interspecific interactions to the model did not enhance explanatory power, intraspecific density dependence clearly stands out as the main variable driving the changes in population sizes across species at the local scale (Table 1 and Figure 2).

In contrast, the neutral theory of biodiversity (Hubbell, 2001) proposes that species can coexist (if only temporarily so) by assuming functional equivalence among species. However, this theory assumes population dynamics to be solely driven by demographic stochasticity and dispersal (Chesson, 2000; Mittelbach, 2012), which is not supported by our findings. Note that, within species, census errors cause autocorrelations in time-series data that can artificially increase the observed strength of intraspecific density dependence (Freckleton et al., 2006), while across species, census errors inflate the variance of the data and can decrease the cross-correlations among species. However, density regulation appears to be important in temperate bird species (Sæther et al., 2008), operating through both survival and reproduction (e.g., Grøtan et al. 2009; Perrins, 1979; Sæther et al., 1998), and recent studies have emphasized its importance for the structure and stability of communities (Adler et al., 2018; Kuang et al., 2017; Sæther et al., 2016; van Altena et al., 2016), thus further supporting our findings.

Observations of interspecific interactions at finer scales

While modeling interspecific interactions did not improve explanatory power, it does not mean that interspecific interactions do not take place or are not important. The influence of species interactions acts on the level of the individual and might not be captured by large-scale data. Many studies investigating species interactions are carried out on a much finer scale, and in a setting where interactions may be more likely to occur. For instance, supplementary feeding is known to increase population sizes to (artificially) higher levels (e.g., Källander, 1981; Robb et al., 2008), likely intensifying competition at such easily accessible study sites (Francis et al., 2018). Nesting boxes may also be preferred over natural alternatives, further intensifying competition. Several studies have shown that e.g., the Blue Tit and the Great Tit compete over nest boxes (e.g., Minot & Perrins, 1986; Newton, 1994), but in a natural setting, their nest-site preferences, while overlapping, differ (Minot & Perrins, 1986). Competition observed in these settings may thus be relatively localized and might not be representative for the avian community in general.

Fluctuating environments

Temperature and precipitation had a comparably small effect on the species' population fluctuations (Table 2), even if we included the best possible climate windows for each species in each plot separately. The contribution of habitat and log area to the total variance were also relatively small. Note that at larger spatial scales, the variance contributions simply changed in response to the changes made to the predictor variable density dependence.

Our models simultaneously include the effect of variables acting both within and across plots, and variables such as temperature and precipitation that might have a strong effect within single plots can appear to be less important as the focus is moved to a more general picture, as we do here. Previously, Mutshinda et al. (2009), detected a large effect of environmental factors on community composition across taxa, but environmental variance in their study includes both fixed weather variables and also, e.g., random and area effects.

The random plot effect constituted a relatively prominent proportion of the variation even at the local scale, indicating permanent variation in habitat suitability among plots. The importance of the random plot effect increased proportional to the decreased ability of density dependence to explain the growth rates of the local populations as the spatial scale of interactions is increased (Table 2), emphasizing the importance of the scale at which community dynamics are being studied.

The temporal random effect caused by environmental stochasticity (Lande et al., 2003) explains annual variation in community abundance across sites. Compared to the fixed environmental effects, the spatially structured temporal random effect explained more of the total variation, indicating that other environmental factors than those included in our model, have an additional effect on the single species dynamics. One such variable is the so-called beechmast. In large parts of Europe, seeds from the beech (*Fagus sylvatica*) are an important, annually highly variable, food source for many birds during winter, and is known to strongly influence next years' densities for many species (Chamberlain et al., 2007).

It is also known that an incorrect specification of density regulation can lead to biased estimates of environmental effects (Lindén et al., 2013). Here, we observed that especially the estimations of the contributions from the two random effects were affected by the degree of spatial smoothing of the density predictor variables. We also note that, in spatial models, the environmental predictors and the spatial random effect can be partially confounded with each other, a phenomenon called spatial confounding (Hanks et al., 2015; Marques et al., 2021). However, we did not find signals of spatial confounding in our study (see Appendix S4).

It is very difficult to capture the patterns observed in nature in all its complexity by the use of simple models. Important factors may remain unaccounted for, and noise in the data generated by, e.g., demographic stochasticity and observational errors might be quite strong. However, the current implementation of HMSC does not allow for the estimation of demographic stochasticity, see Ovaskainen and Abrego (2020: 39).

In summary, utilizing a Joint Species Distribution Modeling approach to investigate the factors structuring a temperate bird community, we found intraspecific density dependence to be of great importance for community composition locally, while climate variables accounted for a small proportion of the variation in the composition of the bird communities. Including species interactions did not result in a better explanatory power or predictive power at any spatial scale. The observed pattern of weak inter- but strong intraspecific density dependence is in line with expectations from the theory of niche differentiation. Thus, it is advisable to conduct model selection prior to including interspecific interactions into community models, in terms of developing efficient models while avoiding overparametrization. At the same time, heterogeneity in the dynamics of single species, especially density dependence, is important to include to obtain a realistic understanding of community changes over time occurring at different spatial scales.

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CONFLICT OF INTEREST

The authors declare no conflictof interest.

DATA AVAILABILITY STATEMENT

Data (Freeman et al., 2007; Marchant et al., 1990) as well as a table of model selections for climate variables (Sandal et al., 2022) are available in Dryad at https://doi.org/10.5061/dryad.crjdfn34r

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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Appendix S1: Species list

Appendix S1: Table S1. List of bird species commonly encountered in the UK investigated in the here presented study (n=60 species).

Species name	English name
Turdus merula	Blackbird
Sylvia atricapilla	Blackcap
Cyanistes caeruleus	Blue Tit
Pyrrhula pyrrhula	Bullfinch
Buteo buteo	Buzzard
Corvus corone	Carrion Crow (Inc. Hooded Crow)
Fringilla coelebs	Chaffinch
Phylloscopus collybita	Chiffchaff
Periparus ater	Coal Tit
Streptopelia decaocto	Collared Dove
Cuculus sp.	Cuckoo
Prunella modularis	Dunnock
Sylvia borin	Garden Warbler
Regulus regulus	Goldcrest
Carduelis carduelis	Goldfinch
Locustella naevia	Grasshopper Warbler
Dendrocopos major	Great Spotted Woodpecker
Parus major	Great Tit
Picus viridis	Green Woodpecker
Chloris chloris	Greenfinch
Perdix perdix	Grey Partridge
Passer domesticus	House Sparrow
Corvus monedula	Jackdaw
Garrulus glandarius	Jay
Falco tinnunculus	Kestrel
Vanellus vanellus	Lapwing
Dryobates minor	Lesser Spotted Woodpecker
Sylvia curruca	Lesser Whitethroat
Linaria cannabina	Linnet
Athene noctua	Little Owl
Aegithalos caudatus	Long tailed Tit
Pica pica	Magpie
Poecile palustris	Marsh Tit
Turdus viscivorus	Mistle Thrush
Sitta europaea	Nuthatch
Phasianus colchicus	Pheasant
Motacilla alba	Pied Wagtail
Alectoris rufa	Red legged Partridge
Acanthis flammea	Redpoll

Emberiza schoeniclus	Reed Bunting
Erithacus rubecula	Robin
Acrocephalus schoenobaenus	Sedge Warbler
Alauda arvensis	Skylark
Turdus philomelos	Song Thrush
Accipiter nisus	Sparrowhawk
Muscicapa striata	Spotted Flycatcher
Sturnus vulgaris	Starling
Columba oenas	Stock Dove
Hirundo rustica	Swallow
Strix aluco	Tawny Owl
Certhia familiaris	Treecreeper
Anthus trivialis	Tree Pipit
Passer montanus	Tree Sparrow
Streptopelia turtur	Turtle Dove
Sylvia communis	Whitethroat
Poecile montanus	Willow Tit
Phylloscopus trochilus	Willow Warbler
Columba palumbus	Woodpigeon
Troglodytes troglodytes	Wren
Emberiza citrinella	Yellowhammer

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Appendix S2: Supporting information on the model structure

Appendix S2: Section S1

We utilize the model described in detail in Ovaskainen et al. 2017. Please see also Ovaskainen and Abrego (2020).

The foundation for our analysis is the standard first order multivariate autoregressive model MAR(1), specified as follows:

$$y_{i,t} = c_i + \sum_{j=1}^{m} \alpha_{i,j} y_{j,t-1} + e_{i,t} \tag{1}$$

Where $y_{i,t}$ is the log-abundance of species i at time t. c_i denotes the intercept, and $\alpha_{i,j}$ is the interaction coefficient, and $e_{i,t}$ is the noise term. In the HMSC framework, we build this model for all species simultaneously. Writing equation 1 in vector form for all species:

$$\boldsymbol{y_t} = \boldsymbol{c} + \boldsymbol{A}\boldsymbol{y_{t-1}} + \boldsymbol{e_t} \tag{2}$$

Assuming a normal distribution of the data on the log-scale, we model the abundance of species *i* in plot *p* at time *t* as a draw from the normal distribution,

$$y_{ipt} \sim N(L_{ipt}, \sigma_i^2) \tag{3}$$

The linear predictor includes a fixed (L_{ipt}^F) and random (L_{ipt}^R) term, as well as some residual error. The fixed part may further be decomposed into an environmental term (L_{ipt}^E) and a species association term (L_{ipt}^A), so that $L_{ipt}^F = L_{ipt}^E + L_{ipt}^A$.

In further detail, the environmental term is described as:

$$L_{ipt}^{E} = \sum_{j=1}^{n} x_{jpt}\beta_{ij} \quad (4)$$

where x_{jpt} is the covariate j (out of n covariates) at plot p at time t, and β_{ij} is the response of species i to covariate j. The vector of regression coefficients for species i is modelled further as:

$$\beta_{i.} \sim N(\mu_{i}, \mathrm{V}) \quad (5)$$

where $\mu_{i.}$ is the expected environmental niche for species i and the variation in the expected niche is V, a matrix of nxn dimensions. In V, the variance in the species' response to the environmental covariates is found on the diagonal, and the covariance in the species' response to pairs of covariates is found on the off-diagonals. Here, we assume $\mu_{i.}$ to be equal for all species.

We modelled species interactions as

$$L_{ipt}^{A} = \sum_{j=1}^{m} \alpha_{ij} y_{jpt-1}, \quad (6)$$

where m is the number of species, α_{ij} models the effect of species j on species i, and y_{jpt-1} is the standardized, log-transformed density of species j at plot p the previous year. The interaction term α_{ij} was specified differently for the different variants of the model, described in the main text and in more detail below. For completeness, we include the description of all four model variants here, even if some of the information is presented in the main text also.

Model Variant M1: No inter-specific interactions.

Only diagonal elements α_{ii} that model intra-specific density dependence were estimated, whereas the effects of interspecific interactions were excluded by fixing $\alpha_{ij} = 0$ for $i \neq j$.

Model Variant M2: Full interactions.

We included as predictors the densities of all the species in the previous year, thus estimating a full matrix of species-to-species interaction coefficients. In this case, the interaction coefficients α_{ij} were estimated for every pair of species as free parameters, assuming an independent normally distributed prior for each parameter.

Model Variant M3: Sparse interactions.

We assigned for interaction coefficients α_{ij} a multiplicative prior

$$\alpha_{ij} = p_{ij}\,\hat{\alpha}_{ij}. \tag{7}$$

The prior for the first factor is p_{ij}~Bernoulli(0.1), so this models whether the interaction is zero (with prior probability 0.9) or non-zero (with prior probability 0.1). For cases where the interaction is non-zero, the second factor $\hat{\alpha}_{ij}$ has the same normally distributed prior as in Model Variant 2.

Model Variant M4: Community level drivers.

We modelled interspecific competition α_{ij}, implemented through a latent variable approach, as follows:

$$\alpha_{ij} = \sum_{k=1}^{n_d} q_{i,k} w_{k,j} + \delta_{ij}\iota_i \tag{8}$$

Herein, species are assumed to contribute to one or more of n_d "community-level drivers", defined as linear combinations of species densities, ecologically corresponding to e.g. total community biomass. The term $w_{k,j}$ models the contribution of species j to driver k and the term $q_{i,k}$ the influence of this driver on species i. Here, $w_{k,j}$ is treated as the latent factors, and $q_{i,k}$ as the factor loadings.

Additional effects of intra-specific interactions ι_i (beyond those captured by the community-level drivers) are added to the interaction matrix via the Kronecker's delta δ_{ij}which is 1 for

δ_{ii}, and otherwise 0. We assumed the prior of Ovaskainen et al. (2017) that increases shrinkage with the index of the driver and fixed the number of drivers to two.

Finally, the random term is defined as

$$L_{ipt}^{R} = \sum_{j=1}^{n} r_{ipt}^{j}, \tag{9}$$

i.e. the sum of *n* random effects (r_{ipt}^{j}) included in the model. In HMSC, the random effects are modeled using a latent variable approach, greatly reducing the amount of parameters. See Ovaskainen and Abrego (2020, Ch. 4) for details.

Here, we defined 2 random effects: r_{ipt}^{1}, the spatial (plot) and r_{ipt}^{2}, the temporal (year) random effect. For both our spatial and temporal random effects, we specify an exponentially decaying structure in the latent factors, which is based on the exponentially decaying covariance function $f(d) = \sigma_S^2 \exp{(-d/\alpha)}$, where σ_S^2 is the spatial variance, *d* the distance between plots (in the case of the temporal random effect, *d* refers to the distance in time between sampling events) and α is the spatial scale of autocorrelation.

Latent variables can capture unexplained autocorrelation in the response variable that can either be due to e.g. environmental factors inducing population synchrony (Moran effect) that were not accounted for in the fixed part, or due to species associations. In this way, the residual variance-covariance matrix from the random term may, with careful consideration, be interpreted as possible species interactions. However, in this paper, we choose to model the species interactions directly in the fixed term rather than relying on the residual variance-covariance matrix from the random term.

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Appendix S3: Supporting information on linear transformations of the data

Appendix S3: Section S1

Let n_{ipt} be the count for species i in plot p at year t. We first converted the count data into log-transformed species densities as:

$o_{ipt} = \log((n_{ipt}+1)/A_p)$, (1)

where A_p is the area of plot p and we added 1 to n_{ipt} to assure positive values. We subsequently scaled the o data for each species i by the transformation

$u_{ipt} = b_i\,(o_{ipt} - a_i)$, (2)

where a_i and b_i were chosen to make the data for each species to have zero mean and unit variance (over all sampling units). In other words, in this step the species mean (a_i) is subtracted from the log-transformed species densities, and subsequently divided by the species' standard deviation ($1/\,b_i$).

After this transformation, the summed density of all species ($\sum_{it} u_{ipt}$) decreased with the area of the plot. This is likely to be partially the case because smaller plots are on average of higher quality (per unit area) than large plots, in part because smaller plots are likely to be surveyed more thoroughly than large plots. We account for this systematic variation by adding a plot-specific constant:

$y_{ipt} = k_p + u_{ipt}$, (3)

so that $\sum_{it} y_{ipt} = 0$, i.e. all plots have the same average summed species density. k_p is the negative plot mean of u across all species and years within a plot, i.e. $k_p = -\left(\frac{1}{n_i \times n_t}\right) \times \sum_{it} u_{ip}$, where n_i is the number of species and n_t is the number of years in the plot (note that the number of species included in the analyses is the same for all plots). In the model, y is used as the response variable.

As explained above, the original count data n is translated into the standardized log-density y using three linear transformations. As we fit linear models that include intercepts and slopes and the random effect of the plot, these transformations are redundant in the following sense: For instance, if fitting a model to the original log-density o instead of the standardized log-density y, the model would be mathematically equivalent (the parameters of the model fitted for o can be mapped to those of the model fitted for y). The transformations were performed to increase the interpretability of model parameters: y measures variation in species log-density in the same units for all species: in units of standard deviation that each species shows in the data. Further, as y is standardized to have zero mean over all species within each plot, a positive mean value of a focal species in a particular plot means that, compared to the other species in the community, the focal species is more abundant than the average of that plot.

Supporting Information. Sandal, Lisa, Vidar Grøtan, Bernt-Erik Sæther, Robert P. Freckleton, David G. Noble and Otso Ovaskainen. 2022. "Effects of Density, Species Interactions and Environmental Stochasticity on the Dynamics of British Bird Communities." Ecology e3731. https://doi.org/10.1002/ecy.3731

Appendix S4: Supporting information on the spatial scaling of the spatial random effect

Appendix S4: Table S1. The spatial scales of exponential decay of the spatial random effect (denoted *r* here, equivalent to the α parameter of HMSC; Ovaskainen and Abrego 2020). The table shows, for each model type (M1-M4) and each spatial scale (L-R) at which species interactions are defined, the posterior mean estimate of the *r* parameter (unit: km) related to the leading factor of the spatial random effect, as well as the posterior probability by which there is a spatial signal, i.e., that $r>0$ (note that the prior probability of $r=0$ equals 0.5; see Ovaskainen and Abrego 2020, p. 67).

Model	**Spatial scale**	**E[*r*]**	**P[*r* >0]**
M1	L	558.12	1
M2	L	532.45	.996
M3	L	639.43	1
M4	L	628.42	1
M1	P	0	0
M2	P	0.02	.002
M3	P	0	0
M4	P	.008	.001
M1	A	170.53	0.85
M2	A	157.09	0.27
M3	A	166.05	0.51
M4	A	334.56	0.52
M1	R	452.89	0.76
M2	R	167.46	0.50
M3	R	239.62	0.66
M4	R	4.52	0.25

L (Local scale) = no spatial smoothing, P (Proximal scale) = average distance to the nearest neighboring plot [18 km], A (Average scale) = the average distance between plots [204 km], R (Regional scale) = maximum distance between plots [711 km].

Appendix S4: Section S1.

In spatial models, the environmental predictors and the spatial random effect can be partially confounded with each other, a phenomenon called spatial confounding (Hanks et al. 2015, Marques et al. 2020). If covariates are spatially autocorrelated, estimates of fixed effects of covariates may be biased because the effects of covariates could instead become captured in the spatial random effect. In essence, the spatial random effect and the spatially autocorrelated covariate would be "competing" to explain the same part of the variation. Such spatial confounding can lead to underestimation of the effects of spatially autocorrelated covariates. However, Page et al. (2017) suggested that model predictions would not become worse by spatial confounding.

In our study, we applied varying degrees of spatial smoothing to the density predictor covariate (but not to any other covariates). When applying spatial smoothing to the density covariate, the spatial autocorrelation of this covariate increases. If spatial confounding occurred, this increased autocorrelation could be expected to increase the estimated spatial scaling of the spatial random effect. Here, we found a large-scale spatial signal for the model where spatial scale of the interactions was defined locally, i.e. $P[r>0]$ equal or close to 1 (see Appendix S4: Table S1, spatial scale=L), but weak or no spatial signal in models where the spatial scale of interactions was non-local (spatial scale P-R). (Note that in the prior, the probability of $r=0$ is set to 0.5, and thus if $P[r>0]<0.5$, there is evidence against spatial signal. Thus, we considered there to be strong support for a spatial signal if the posterior probability by which the alpha parameter is positive was at least 0.90. With this criterion, the local models showed strong support for a spatial signal, but the non-local models did not). Thus, in contrast to what might be expected with spatial confounding, here we see that the estimates of the spatial scales of exponential decay of the spatial random effect (E[*r*], Appendix S4: Table S1.) decreased and became non-significant when spatial smoothing was applied to the density predictor variable.

For a given model variant, increasing degree of spatial smoothing reduced both explanatory and predictive power (Table 1). Additionally, the proportion of variation explained by the density covariate decreased while the proportion of variation explained by the spatial random effect increased with increasing degree of spatial smoothing (Table 2). These patterns, in combination with the reduction of spatial scale of the random effect, are more likely linked to the decreasing explanatory power of the density covariate rather than to spatial confounding between this covariate and the spatial random effect.

As an additional test of possible spatial confounding, we tested if estimated spatial random effects were correlated with the predictors related to the fixed effects. We extracted the posterior mean estimate of the leading spatial latent factor and computed its correlation (over all sampling units) with all the predictors included in the model, including the previous year's abundances of all the 60 species. This analysis was done for all 16 models (four model variants times four spatial scales at which the predictors were computed). The results showed that the correlations were essentially normally distributed with mean approximately at 0, with maximal range within [-0.2,0.2] for all four model variants (Appendix S4: Figure S1-S4). This further indicates that spatial confounding was unlikely to be a major issue in the interpretation of our results.

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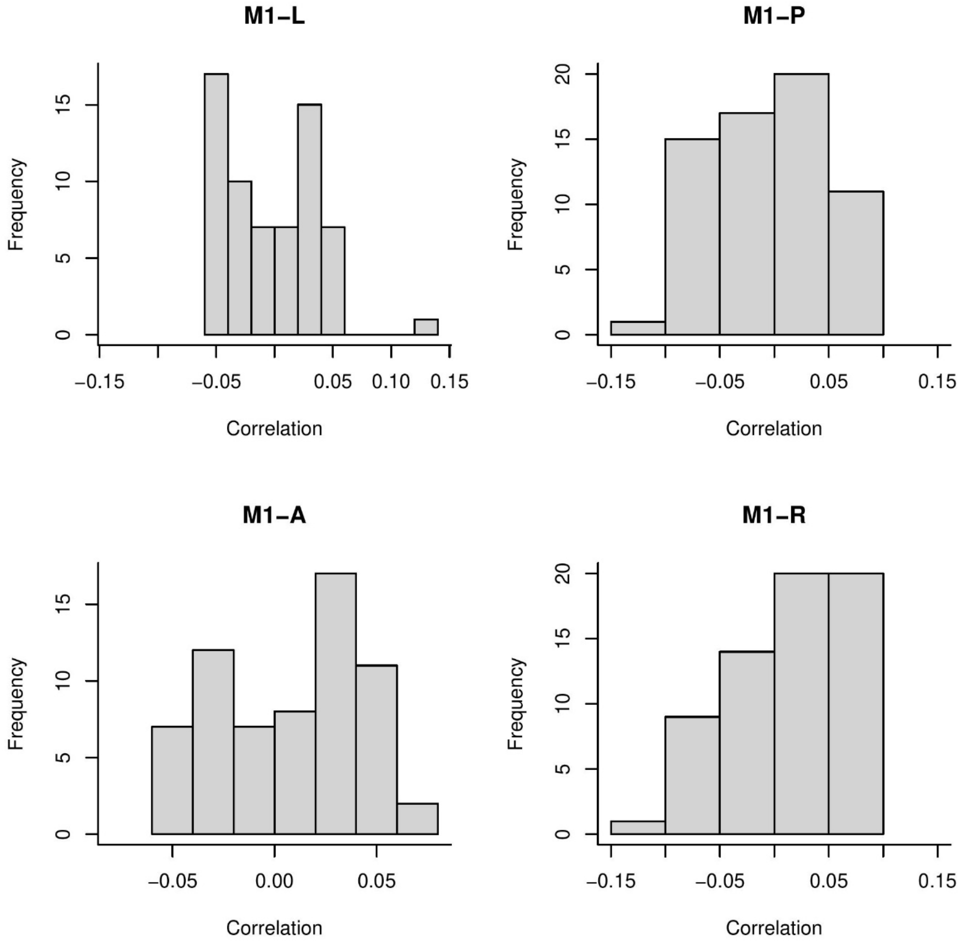
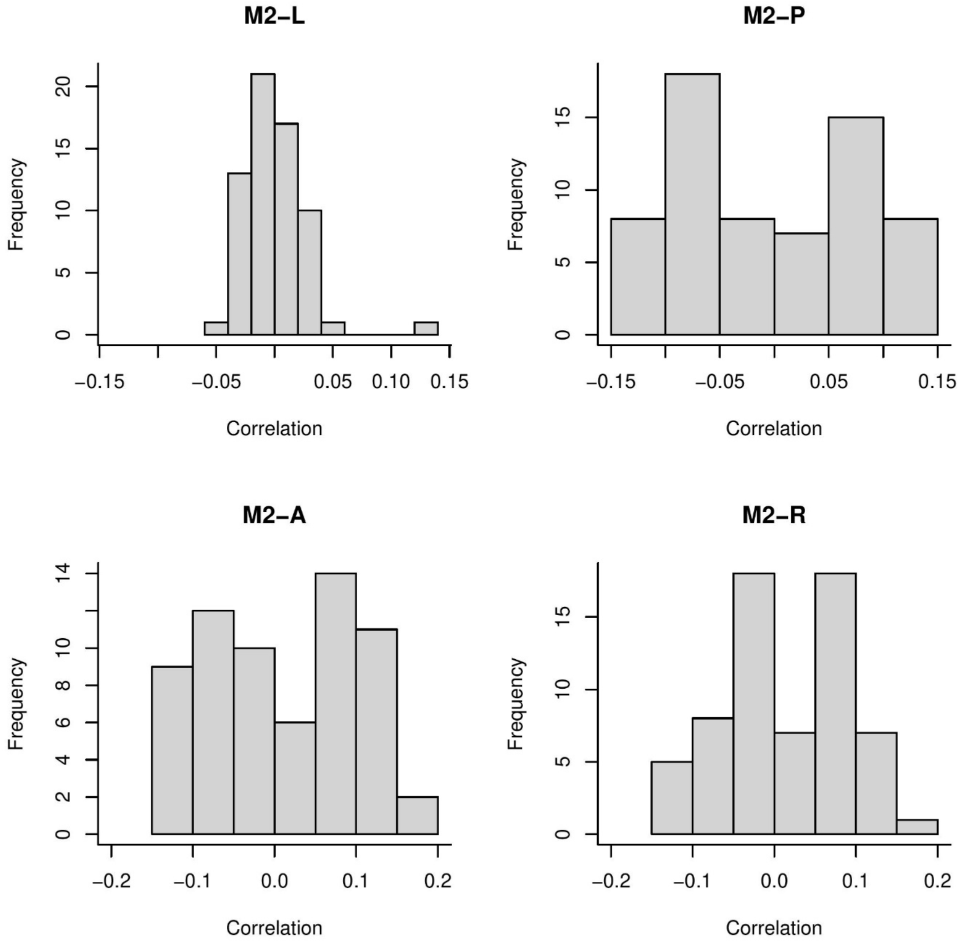
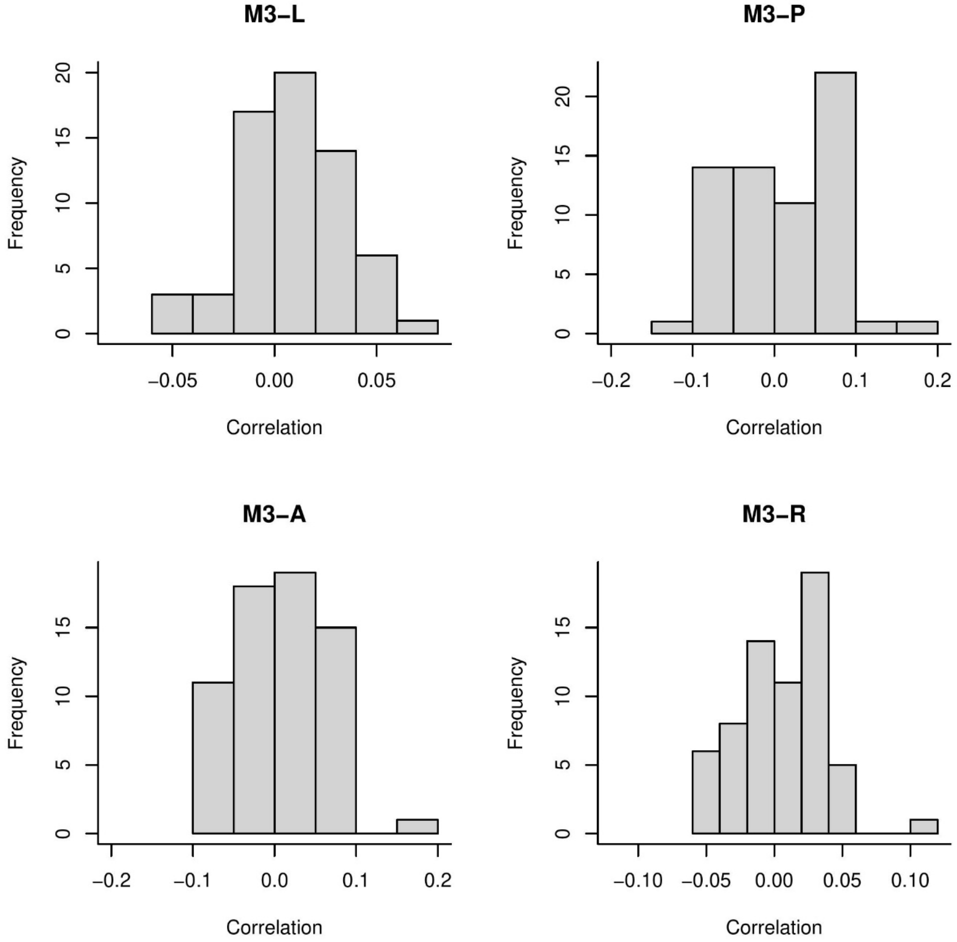


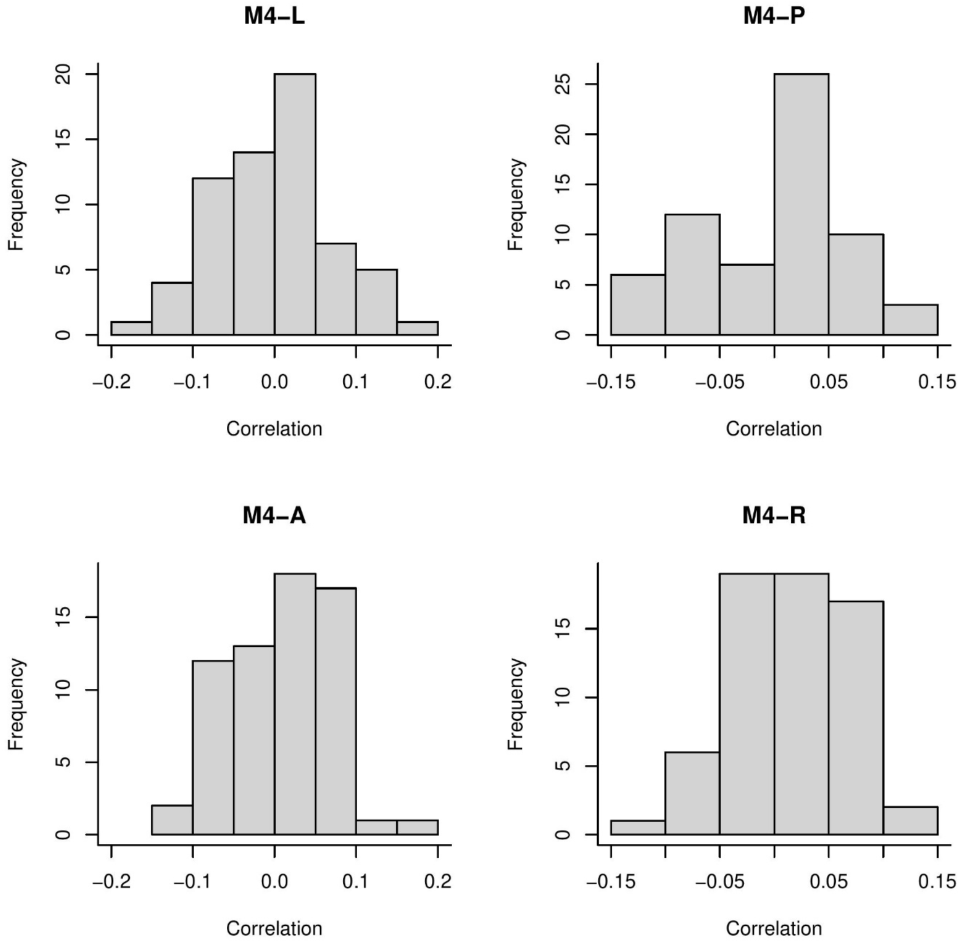
Appendix S4: Figure S1. Distribution of correlation coefficients over all sampling units between the posterior mean estimate of the leading spatial latent factor and all the predictors for model variant 1 (M1) at all spatial scales (L-R), including the previous year's abundances of all the 60 species. L (Local scale) = no spatial smoothing, P (Proximal scale) = average distance to the nearest neighboring plot [18 km], A (Average scale) = the average distance between plots [204 km], R (Regional scale) = maximum distance between plots [711 km].



Appendix S4: Figure S2. Distribution of correlation coefficients over all sampling units between the posterior mean estimate of the leading spatial latent factor and all the predictors for model variant 2 (M2) at all spatial scales (L-R), including the previous year's abundances of all the 60 species. L (Local scale) = no spatial smoothing, P (Proximal scale) = average distance to the nearest neighboring plot [18 km], A (Average scale) = the average distance between plots [204 km], R (Regional scale) = maximum distance between plots [711 km].



Appendix S4: Figure S3. Distribution of correlation coefficients over all sampling units between the posterior mean estimate of the leading spatial latent factor and all the predictors for model variant 3 (M3) at all spatial scales (L-R), including the previous year's abundances of all the 60 species. L (Local scale) = no spatial smoothing, P (Proximal scale) = average distance to the nearest neighboring plot [18 km], A (Average scale) = the average distance between plots [204 km], R (Regional scale) = maximum distance between plots [711 km].



Appendix S4: Figure S4. Distribution of correlation coefficients over all sampling units between the posterior mean estimate of the leading spatial latent factor and all the predictors for model variant 4 (M4) at all spatial scales (L-R), including the previous year's abundances of all the 60 species. L (Local scale) = no spatial smoothing, P (Proximal scale) = average distance to the nearest neighboring plot [18 km], A (Average scale) = the average distance between plots [204 km], R (Regional scale) = maximum distance between plots [711 km].

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Appendix S5: Supporting information on the variance partitioning

Appendix S5: Section S1

Supporting information on the function computeVariancePartitioning(), see Ovaskainen and Abrego (2020). This function determines the magnitude of the contribution of each covariate (or group of covariates, if desired) to the total explained variance. The variance partitioning is conducted at the level of the linear predictor in HMSC. Recall that the variance of the weighted sum of X and Y, two random variables can be expanded as:

$$\mathrm{Var}[a\mathrm{X} + b\mathrm{Y}] = a^2\mathrm{Var}[\mathrm{X}] + b^2\mathrm{Var}[\mathrm{Y}] + 2ab\mathrm{Cov}[\mathrm{X}, \mathrm{Y}], \tag{1}$$

Cov[X, Y] being the covariance between the two. Thus, the variance in the linear predictor can be expanded as follows:

$$\mathrm{Var}[\mathrm{L}] = \sum_{k=1}^{n_c} \beta_k^2 \mathrm{Var}[x_{\cdot k}] + 2\sum_{k_1=1}^{n_c-1} \sum_{k_2=k_1+1}^{n_c} \beta_{k_1}\beta_2 \,\mathrm{Cov}[x_{\cdot k_1}, x_{\cdot k_1}], \tag{2}$$

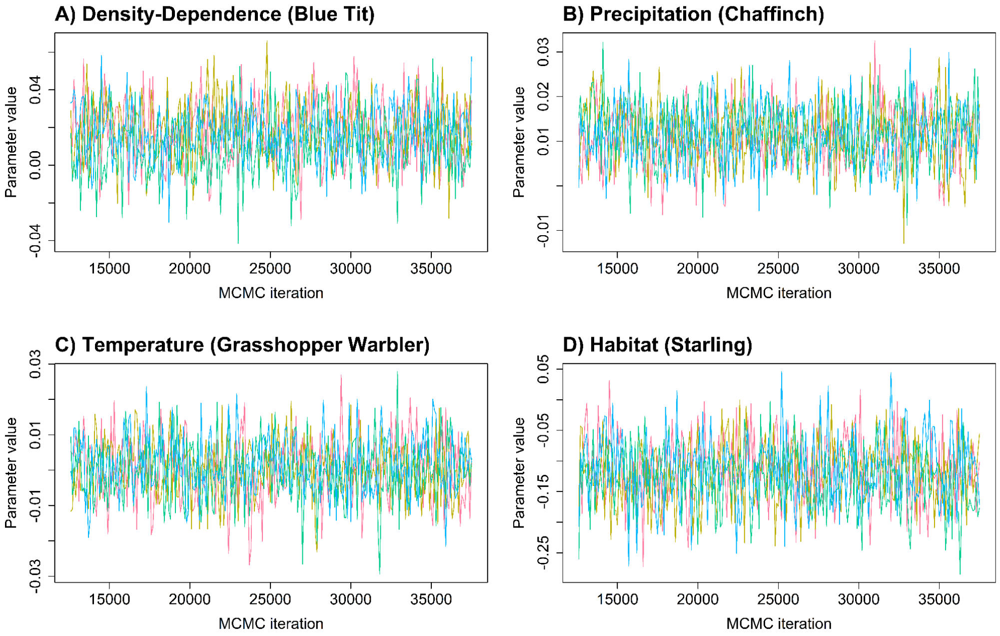
with *k* explanatory variables (*x*). The dot notation in $x_{\cdot k}$ means that $x_{\cdot k}$ is the vector consisting of the x_{ik} values for all sampling units i. Expanding the variance in this way allows us to separately analyze the magnitude of contribution to the explained variance by each covariate.

Literature cited

Ovaskainen, O., and N. Abrego. 2020. Joint Species Distribution Modelling: With Applications in R. Cambridge University Press. Cambridge, Cambridgeshire, UK

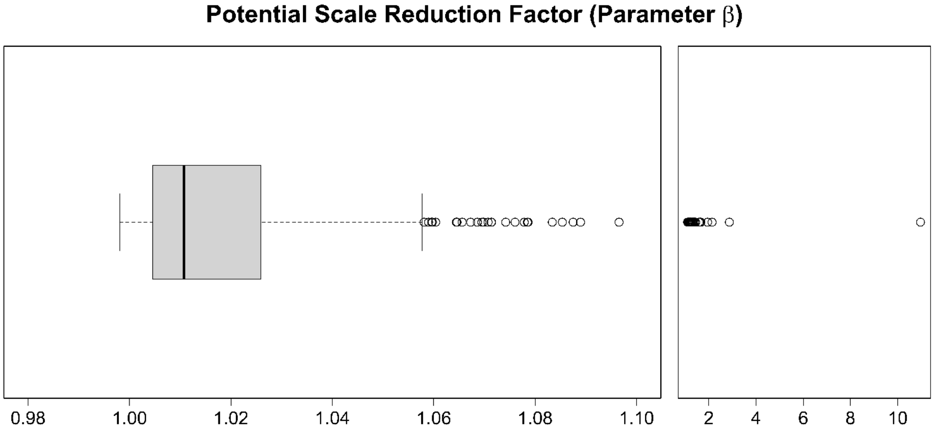
Supporting Information. Sandal, Lisa, Vidar Grøtan, Bernt-Erik Sæther, Robert P. Freckleton, David G. Noble and Otso Ovaskainen. 2022. “Effects of Density, Species Interactions and Environmental Stochasticity on the Dynamics of British Bird Communities.” Ecology e3731. https://doi.org/10.1002/ecy.3731

Appendix S6: Supporting information on model convergence



Appendix S6: Figure S1. Examples of posterior trace plots for some beta parameters from model M1-L. Panel A) shows intraspecific density dependence for Blue Tit, B) shows precipitation for Chaffinch, C) temperature for Grasshopper Warbler and D) habitat for Starling.

We used the function traplot() from the package “mcmcplots” (Curtis et al., 2018) to generate Figure S5.1.



Appendix S6: Figure S2. Evaluation of MCMC convergence of model M1-L in terms of potential scale reduction factors for the beta parameters, i.e. the estimates of intercepts and species responses to model covariates.

Literature Cited

Curtis, S. M., I. Goldin, and E. Evangelou. 2018. Package ‘mcmcplots’

Supporting Information. Supporting Information. Sandal, Lisa, Vidar Grøtan, Bernt-Erik Sæther, Robert P. Freckleton, David G. Noble and Otso Ovaskainen. 2022. “Effects of Density, Species Interactions and Environmental Stochasticity on the Dynamics of British Bird Communities.” Ecology e3731. https://doi.org/10.1002/ecy.3731

Appendix S7: Simulation study

Appendix S7: Section S1

We generated simulated data containing a clear signal of species interactions at the local scale, to verify the different models’ capacity to pick up such a signal, if existing. The models used in this analysis have all been tested by Ovaskainen et al. (2017), however, it is important to verify that the models are applicable to the data at hand. For instance, it needs to be verified that the time series are long enough.

To ensure stability of the simulated data, we use the real observed values at time t-1 as starting value for each time-step in the simulation, so that:

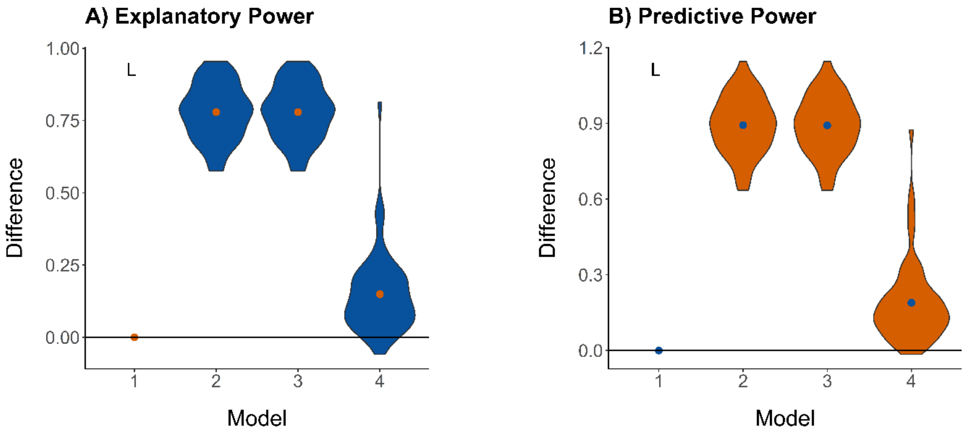
$$\boldsymbol{y_{simulated}} = \boldsymbol{y_{observed,\ t-1}} \times \alpha_{ij} + \boldsymbol{\varepsilon} \qquad (1)$$

where $\boldsymbol{y_{observed,\ t-1}}$ is the matrix containing the observed, log-transformed and standardized densities at time t-1. $\alpha_{ij} \sim N(0,1)$, and is divided by the square root of the number of species, to create a matrix containing relatively weak inter-species density dependencies ($\alpha_{ii} = 0$, thus excluding intra-specific density dependencies in order to keep the simulation as simple as possible), and $\boldsymbol{\varepsilon} \sim N(0,1)$ multiplied by 0.5 is a matrix of relatively weak random error terms.

We subsequently evaluated explanatory and predictive power at the local scale following the same procedure as described above and using the same settings for model fitting as before, apart from setting thin=10 (Appendix S7: Table S1).

Appendix S7: Table S1. Explanatory and predictive power of the models at the local scale (no spatial smoothing). Explanatory power is measured as the mean of the correlation for each species in each plot between simulated time-series and time-series predicted by the different models fit to the simulated data. Predictive power is measured as the mean of the correlation for each species in each plot between simulated time-series and independently predicted time-series obtained by 5-fold cross-validation [results based on thin=10].

		Explanatory Power				**Predictive Power**			
	Model	**M1**	**M2**	**M3**	**M4**	**M1**	**M2**	**M3**	**M4**
Scale	**L**	0.201	0.980	0.979	0.350	0.09	0.980	0.977	0.275



Appendix S7: Figure S1. The difference for each species in **A)** Explanatory power and **B)** Predictive power between the focal model and model M1-L at the local scale (L) for the 4 different models, so that L 1= (M1-L) - (M1-L) = 0, L 2= (M2-L) - (M1-L), L 3= (M3-L) -

(M1-L), L 4= (M4-L) - (M1-L). The mean difference is indicated by a dot. Values for M1-L are exactly zero, since they are being compared with self.

Note that, since the species interactions in our simulation is defined in terms of M2, it is expected that explanatory and predictive power for M4 is substantially less than for M2 and also for M3, the latter performing better at capturing such data compared to M4. While the simulation study could have been extended by simulating the interactions in terms of M4 also, adding this component would be computationally intensive. Since Ovaskainen et al. (2017) performed a simulation study including the interactions in terms of M4 also, and the authors showed that Hmsc can identify the underlying model (and e.g. separate it from the sparse interaction models), adding such a component here would not provide great added value.

In summary, Appendix S7:Table S1 and Figure S1 clearly show that Hmsc is able to pick up the signal of species interactions in the type of data analyzed in this study, if present.

Literature Cited

Ovaskainen, O., G. Tikhonov, D. Dunson, V. Grøtan, S. Engen, B.-E. Sæther, and N. Abrego. 2017. How are species interactions structured in species-rich communities? A new method for analysing time-series data. Proceedings of the Royal Society B: Biological Sciences **284**(1855): 20170768.

Paper II

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Paper III

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