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RESEARCH ARTICLE



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Scale dependency of joint species distribution models challenges interpretation of biotic interactions

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Abstract

Aim: Separating the biotic and abiotic factors controlling species distributions has been a long-standing challenge in ecology and biogeography. Joint species distribution models (JSDMs) have emerged as a promising statistical framework towards this objective by simultaneously modelling the environmental responses of multiple species and approximating species associations based on patterns in their (co-)occurrences. However, the signature of biotic interactions should be most evident at fine spatial resolutions. Here, we test how the resolution of input data affects the inferences from JSDMs.

Location: Switzerland.

Taxon: Birds.

Methods: Using standardized survey data of 43 woodland bird species and 8 climatic, topographic and vegetation structural predictors, we fit JSDMs at different spatial resolutions (125–1000 m) and sampling periods (1 and 5 years). In addition, we calculate functional similarity among all species as an independent proxy of biotic interactions, specifically competition. We then assess how JSDM performance and estimates vary with the spatial resolution of the input data and test whether species associations are consistent across grain sizes and with the alternative approach based on functional similarity.

Results: Our results show better model performance at coarser spatial resolutions and for longer sampling periods. Although pairwise species associations estimated in JSDMs were generally shifted towards positive values, we found a higher proportion of negative associations at fine spatial resolutions. Strikingly, estimates were not consistent across spatial scales and frequently switched between positive and negative values. Moreover, estimated species associations tended to be more positive for functionally similar species.

Main conclusions: Our results show that species associations are more differentiated, that is, cover a broader range of values, at finer spatial resolutions. Yet, their positive correlation with functional similarity and the general over-representation of positive

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associations suggest that shared responses to unobserved environmental predictors rather than biotic interactions underlie these scaling effects, cautioning against a naive interpretation of species associations estimated by JSDMs at any spatial scale.

KEYWORDS

biotic interactions, birds, community assembly, hierarchical modelling, JSDM, spatial scaling

1 | INTRODUCTION

The geographical distribution of species lies at the heart of many questions in ecology, biogeography and nature conservation. Three main assembly processes determine where species occur (Brown, 1995; Soberón & Peterson, 2005): biogeographical history and dispersal delineate regions that are generally accessible to individuals of a species (Soberón, 2007), abiotic environmental conditions outline the physiological limits under which populations of a species can persist (Grinnell, 1917; Hutchinson, 1957) and biotic interactions, such as predation, facilitation or competition, further modify the limits of persistence in the presence of other species (Elton, 1927; Hutchinson, 1957). In addition to these deterministic factors, stochastic processes such as random colonization and extinction or ecological drift create variation among species assemblages under otherwise identical conditions (Chase & Myers, 2011; Hubbell, 2001). While the ecological significance of each of these factors is well established in principle, assessing their relative importance in shaping realized species assemblages remains a major challenge in ecological research (Lawton, 1999: Leibold et al., 2004: Wisz et al., 2013).

One aspect that makes disentangling assembly processes difficult is the spatial scale at which the processes act (McGill, 2010; Wiens, 1989). Macroclimatic conditions, for example, are often accurate predictors of large-scale distributional patterns such as species range sizes or range boundaries, while biotic effects are more important for assembly processes at the local scale, where interactions among individual organisms play out (HilleRisLambers et al., 2012; Ricklefs, 1987; Wisz et al., 2013). Correspondingly, the two predominant frameworks for explaining spatial variation in biodiversity tend to focus on opposite ends of the scale continuum. On the one hand, correlative species distribution modelling (SDM) is mostly concerned with biogeographical scales and expresses the distribution of a focal species as a function of the environment only (Box, 1981; Franklin, 1995; Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000). On the other hand, community ecology traditionally highlights associations in the co-distribution of species at local scales, while largely ignoring the direct effects of environmental conditions (Keddy, 1992; McGill et al., 2006). These conceptual limitations have motivated a new generation of statistical approaches that aim for an integrated representation of assembly mechanisms across scales (Araújo & Luoto, 2007; Kissling et al., 2012; Ovaskainen et al., 2010).

Joint species distribution models (JSDMs) are a multivariate extension of SDMs that simultaneously estimate the environmental responses of multiple species and so-called residual correlations between their occurrences after accounting for the environment (Clark et al., 2014; Hui, 2016; Ovaskainen et al., 2010; Pollock et al., 2014; Warton et al., 2015). These residual correlations, referred to here as species associations, are claimed to capture statistical patterns in the co-distribution of species that are not accounted for by the environmental predictors and hence may be indicative of biotic interactions (Pollock et al., 2014; Warton et al., 2015; Wilkinson et al., 2018). The explicit acknowledgement of the multivariate nature of species assemblages in the structure of JSDMs is a promising avenue towards a more realistic representation of biotic and abiotic factors in empirical ecological models (Clark et al., 2014; Ovaskainen et al., 2017). Simulation studies have shown that JSDMs can indeed recover (symmetric) biotic interactions from distributional data under ideal conditions, that is, when sample size is large, community size is small and environmental heterogeneity is negligible (Zurell et al., 2018). However, in real-world applications, these conditions are rarely met, and patterns in species associations could also indicate missing environmental predictor variables, model misspecification and other confounding factors (Dormann et al., 2018; Pollock et al., 2014; Warton et al., 2015). Also, the signal of biotic interaction can easily get lost at coarse-grain sizes (Araújo & Rozenfeld, 2014; Zurell et al., 2018). Thus, a mismatch between the scale of species interactions and the scale of species observations may limit JSDMs' ability to disentangle the importance of abiotic and biotic factors.

Here, we assess the sensitivity of JSDMs to the spatial scale of input data. Using standardized monitoring data of 43 Swiss woodland bird species collected over a period of 1 and 5 years, we derive community data at four spatial grain sizes (125, 250, 500 and 1000 m). We then fit JSDMs on each dataset and contrast the results with respect to overall model fit, explanatory power of environmental predictors versus species associations, as well as the direction and magnitude of estimated species associations. To explore the latter point in more detail, we correlate the estimated species associations with independently established values of pairwise functional similarity based on eight functional traits. We expect (1) overall higher model fits at coarser-grain sizes due to the reduced impact of local stochastic processes (Chase, 2014). Correspondingly, we expect (2) the explanatory power of the fixed effects (environmental predictors) to be highest at coarse-grain sizes, whereas that of the random effects (basis for calculation of species associations) should explain a larger portion of community variation at finer grains. Furthermore, we hypothesize that (3) the proportion of negative species associations decreases at coarser-grain sizes due to the declining signal of competition in species co-occurrences (Araújo & Rozenfeld, 2014; Zurell et al., 2018). Finally, if JSDM species associations and functional similarity capture the same signal of interspecific competition, we expect (4) a negative correlation between these measures, that is, species with similar traits should compete more strongly for resources and co-occur less often than expected by their response to observed environmental predictors. The strength of this correlation should increase towards finer-grain sizes.

2 | MATERIALS AND METHODS

2.1 | Species data

Species observations were collected by the Swiss monitoring of common breeding birds (Monitoring Häufige Brutvögel, MHB, Schmid et al., 2004). The MHB consists of 267 permanent 1 km² sample squares across Switzerland that are visited three times per breeding season (only two times above the treeline). On-site bird surveys follow a pre-defined transect (4-6 km), along which the locations of all observed individuals are recorded in a simplified territory mapping approach. We used species observations from 1 year (2009) and a 5-year period (2007-2011) to explore the sensitivity of our results to annual fluctuations in community composition and to sample size in general. These sampling periods were chosen as they provided the best compromise between data availability (more digitized territory maps available from 2007 onwards) and temporal match with environmental information (most environmental layers describe conditions prior to 2010). Specific combinations of spatial grain size and sampling period are denoted by subscripts throughout the manuscript; for example, $D_{1000,5}$ and $M_{1000,5}$, respectively, refer to the dataset and the model at 1000 m spatial grain size and 5-year sampling period.

Species lists in MHB are typically reported for the entire sample square at 1 km resolution. Here, we used the raw data of digitized territory maps to additionally derive community composition at finer-grain sizes of 500, 250 and 125 m, perfectly nested within the 1 km sample square. Focusing on forest bird communities, we excluded non-forest-dwelling species based on a recent guild classification of Swiss breeding birds (Strebel et al., 2020) and removed sampling squares (including sub-squares at all resolutions) when they had less than 50% forest cover according to a 100-m raster layer provided by the Swiss forest inventory (Waser et al., 2015). Assuming that the location of territories remains relatively stable throughout the breeding season, we then collapsed the species observations from different visits per year and calculated the polygon centroid for each recorded territory. Finally, we overlaid the territory centroids with the sampling grids to derive species presence/absence data at the four different grain sizes. To avoid model instability

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due to low samples sizes, we only included species with at least 10 observations in both the 1-year and 5-year sampling period and removed sampling units without any observation. The final datasets contained presence/absence data for 43 species across 119 ($D_{1000,1}$) to 27072 ($D_{125,5}$) sampling units.

Functional trait data were obtained from Storchová and Hořák (2018). Since our aim was to approximate interspecific competition by quantifying the overlap in species' Eltonian niches, we focused on traits affecting fitness via growth, reproduction and survival while excluding traits that describe purely morphological or habitat-related characteristics. We followed White et al. (2018) in our final selection and included the following eight functional traits: body mass, clutch size, age at first breeding, young developmental type (altricial/semi-altricial/precocial), nesting behaviour (solitary/semi-colonial/colonial), nest type (ground/hole/open arboreal/closed arboreal/ground closed/nest parasite), migratory behaviour (seden-tary/migratory) and diet (folivore/frugivore/granivore/arthropods/ other invertebrates/fish/other vertebrates/carrion/ omnivore).

2.2 | Environmental data

We calculated mean environmental conditions at each grain size based on 100 m raster layers of climate, topography and vegetation structure (for details see Table S1 and data description in Zurell, Zimmermann, et al., 2020). Climatic conditions were derived from daily measurements conducted by the Federal Office of Meteorology and Climatology MeteoSwiss, which were interpolated to a 100 m resolution using the software DayMet (Thornton et al., 1997). Topographic variables were calculated from a 100 m digital elevation model of Switzerland. Vegetation structure was characterized based on multiple-season aerial LiDAR measurements between 2000 and 2007, which were processed in the LAStools software (Isenburg, 2015).

Because in JSDMs all species share a common set of predictor variables, we performed a principal component analysis (PCA) of the 44 candidate variables to identify a subset that best captures all dimensions of environmental variation. To do so, we ranked the variables according to their loadings at each PCA axis and, starting with the first axis, sequentially recorded the variable with the highest loading and removed it from all other rankings. Following Dormann et al. (2013), we then calculated Spearman's rank correlation among all variable pairs and removed the variable with the lower rank if p < 0.7, thus leaving only the most informative uncorrelated environmental predictors at each spatial grain. To ensure the comparability of results across spatial resolutions, we kept only variables that were selected at all four grain sizes, which included five bioclimatic (BIO3: isothermality, BIO5: max. temperature of warmest month, BIO15: precipitation seasonality, BIO19: precipitation of coldest quarter and MIND: yearly moisture index), one vegetation structural (CV: coefficient of variation of LiDAR returns) and two topographic (ASP: aspect and TPI: topographic position index) variables (see digital appendix for details).

2.3 | Statistical modelling

We used probit JSDMs to model species presence/absences at different grain sizes as a function of the same eight pre-selected predictor variables (linear and quadratic terms). Models were fitted with the *Hmsc* R-package (Tikhonov, Opedal, et al., 2020), which implements the hierarchical modelling of species communities (HMSC) framework of Ovaskainen et al. (2017). *Hmsc* allows for fitting JSDMs of large communities and different response types at reasonable computation times (Norberg et al., 2019; Wilkinson et al., 2019). In particular, *Hmsc* supports the specification of random effects that can account for spatial and temporal non-independence in the data, which was necessary to represent our nested study design.

In the HMSC framework, species associations are estimated by means of latent random effects, which capture community variation that is not accounted for by the environmental predictors. The species association matrix is then derived from the correlation in species' loadings on the fitted latent variables. We base our analysis on the species associations derived from the latent random effects associated with the sampling unit, that is, the (sub-) squares for which species occurrences were modelled. Depending on the spatial grain and sampling period, we specified additional random effects to account for the nestedness of sub-squares within the 1 km sample square (if grain size was smaller than 1000 m) and inter-annual variation in species observations (if the sampling period was longer than 1 year). We ran eight parallel MCMC chains per model, with a burn-in of 5000 steps followed by 25,000 sampling steps with a thinning rate of 50, summing up to a total of 4000 samples per model parameter. Models for species abundances with a guasi-Poisson error distribution were explored, but showed poor convergence and were subsequently excluded from the analysis.

We assessed model convergence based on MCMC trace plots (Plummer, 2017), Gelman-Rubin statistics and effective sample size of randomly selected parameters (note that JSDMs estimate a large number of parameters). Model fit was evaluated based on AUC and Tjur's R^2 (Tikhonov, Opedal, et al., 2020). To assess the relative importance of different processes affecting community composition, we further decomposed the explained variance (Tjur's R^2) into components related to the fixed effects (environmental predictors) and random effects (sampling unit, 1 km sample square, year) using tools available in *Hmsc* (Tikhonov, Opedal, et al., 2020). The out-of-sample predictive performance was assessed by calculating AUC and Tjur's R^2 on observations from the 3 years subsequent to the last year included in the training data (2010–2012 for the 1-year models and 2012–14 for the 5-year models).

2.4 | Analysis

For each model, we computed the matrix of pairwise species associations and classified estimates as having high statistical support (or being "significant") if their 95% credible interval did not include zero. We then used summary statistics and visualizations to contrast species associations estimated at different spatial grain sizes and sampling periods.

As an independent proxy for potential biotic interactions, we calculated pairwise functional similarities as 1 – Gower distance (Gower, 1971) based on the eight selected functional traits (see section *Species data*). The levels within categorical traits were weighted such that each trait had a total weight of 1. Note, however, that functional similarity should be mostly an indicator of interspecific competition, as species with a larger niche overlap compete more strongly for the same resources (Gause, 1934; MacArthur & Levins, 1967), whereas other biotic interactions such as mutualism, commensalism or predation are more difficult to infer from functional trait data (but see, e.g. Pichler et al., 2019). We quantified the correlation between the resulting similarity matrix and the species association matrices using Mantel test statistics (Mantel, 1967).

All analyses were performed in R 3.6.2 with the aid of highperformance computing infrastructure. Models were fitted in parallel on 64 cores (2 sampling periods * 4 spatial grain sizes * 8 MCMC chains) with runtimes ranging from 4 h ($M_{1000,5}$) to 14.5 days ($M_{125,5}$). An ODMAP protocol (Zurell, Franklin, et al., 2020) of our analysis is available in the supplementary information.

3 | RESULTS

In-sample predictive performance of JSDMs was highly scale dependent, with overall better model fits on coarse-grained data covering multiple years (Table 1). Mean AUC values across species ranged from 0.85 ($M_{125,1}$) to 0.92 ($M_{1000,5}$) and mean variance explained across all species (R^2) ranged from 0.11 ($M_{125,1}$) to 0.41 ($M_{1000,5}$). However, there was substantial variation in partial model fits for individual species (Table 1, see digital appendix for details), with overall higher values for prevalent species, for example, the great tit (*Parus major*, $\overline{R^2}_{125,1} = 0.23$, $\overline{R^2}_{500,1} = 0.66$), than for species with low population densities, for example, the sparrow hawk (*Accipiter nisus*, $\overline{R^2}_{125,1} = 0.002$, $\overline{R^2}_{1000,1} = 0.12$) (Figure S1). Out-of-sample predictive performance was generally lower than in-sample predictive performance and tended to peak at intermediate-grain sizes (Figure S2).

Variance partitioning identified environmental conditions as the most important predictor of community composition at all grain sizes and sampling periods (Table 1). The random effect associated with the sampling unit (which yields the species association matrix) contributed up to one third to the total explained variance and showed the highest relative contributions at a grain size of 250 m and the longer sampling period of 5 years. Again, there was considerable variation across species (Table 1, see digital appendix for details). For example, the explained variance for the common redpoll (*Acanthis flammea*) and the great tit (*Parus major*) was almost exclusively accounted for by environmental conditions, whereas species associations were the dominating factor for some (fewer) other species, for example, the common chaffinch (*Fringilla coelebs*) or the European robin (*Erithacus rubecula*).

TABLE 1 Variance partitioning for JSDMs fitted at different grain sizes and sampling periods. Values summarize overall model fit (coefficient of discrimination, Tjur's R^2) and the individual contribution of fixed (Environment) and random effects (Species associations, Plot, and Year) across 43 Swiss bird species. Median and 5/95 percentiles are reported

				Variance decomposition (proportion of explained variance)			
Grain size (m)	Sampling period (years)	Sampling units	Total variance explained	Environment	Species associations	1-km sample square	Year
125	1	5656	0.1 (0.01-0.22)	0.72 (0.26-0.96)	0.12 (0.02-0.56)	0.13 (0.02–0.32)	-
250	1	1743	0.24 (0.03-0.44)	0.71 (0.28-0.96)	0.15 (0.01-0.54)	0.09 (0.02-0.27)	-
500	1	467	0.3 (0.08–0.59)	0.8 (0.39–0.97)	0.12 (0.01-0.51)	0.06 (0.01-0.23)	-
1000	1	119	0.37 (0.14-0.59)	0.95 (0.62–0.99)	0.05 (0.01-0.38)	-	-
125	5	27072	0.12 (0.01-0.3)	0.55 (0.15-0.87)	0.2 (0.03-0.69)	0.15 (0.07–0.31)	0.03 (0-0.2)
250	5	8204	0.3 (0.03-0.47)	0.49 (0.19-0.83)	0.34 (0.09-0.69)	0.11 (0.02–0.27)	0.02 (0-0.12)
500	5	2183	0.39 (0.1-0.59)	0.58 (0.26-0.89)	0.24 (0.05-0.56)	0.09 (0.02-0.37)	0.01 (0-0.09)
1000	5	552	0.41 (0.13-0.65)	0.76 (0.46-0.96)	0.23 (0.04-0.52)	-	0.02 (0.01-0.06)

The further analysis of species associations revealed generally higher statistical support on fine-grained, long-term data than on coarse-grained, short-term data (Figure 1). Moreover, the vast majority of significant species associations were positive and close to 1, whereas significant negative species associations were only found in the 5-year datasets, especially at finer-grain sizes (Figure 1).

As indicated by Figure 1, estimated species associations varied across models. Directly contrasting these estimates further confirmed the scale dependency of our results, as species associations estimated at one grain size often did not correspond to those estimated at another grain size (Figure 2). This discrepancy was larger with an increasing difference in grain size. For example, the contrast of species associations from M_{125} and M_{250} was relatively well balanced around the identity line, although a slight bias towards the lower right corner indicates a tendency towards more positive estimates in M_{250} (Figure 2, second column). On the other hand, there was hardly any statistical relationship when contrasting the species associations from M_{125} and M_{1000} (Figure 2, fourth column). Also, many species associations were significant at only one of the two grain sizes (orange and purple circles, Figure 2). Only estimates with high support at both grain sizes (black circles, Figure 2) tended to agree most of the time, at least with respect to the direction of the association (Figure 2, lower left and upper right corners). We found a small number of switches from significant negative (at fine grains) to significant positive (at coarser grains) values at the 5-year sampling period (Figure 2, lower right corner). A switch from significant positive (fine) to significant negative (coarse) was only observed for three species pairs in the 125 m versus 1000 m contrast at 5 years sampling period (Figure 2, upper left corner). These switches were largely driven by two species, as 14 of 16 species pairs switching from negative to positive association involved the citril finch (Serinus citrinella), while all three species pairs switching from positive to negative association involved the dunnock (Prunella modularis) (see SI Tables S1 and S2).

We correlated species associations with pairwise functional similarity to assess whether both measures yield a similar characterization of potential biotic interaction. The observed statistical relationship was weak at coarse-grain sizes but became more evident at finer grains, with a maximum mantel correlation of 0.30 and 0.33 at $D_{125,5}$ and $D_{125,1}$ respectively (Figure 3). Unexpectedly, the direction of this relationship was positive, meaning that species with similar functional traits followed similar distributional patterns (as modelled by the latent random variables) even after accounting for observed environmental predictors. Note, however, that species associations were shifted towards positive values, often lacking negative values below -0.5 (Figure 1).

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4 | DISCUSSION

The general aim of this study was to evaluate how scale decisions affect the conclusions that can be drawn from joint species distribution models. Our hypotheses were framed around the assumption that the spatial signature of biotic interactions, especially that of competition, should be most evident at fine spatial grain sizes and vanish when communities are defined at coarser resolutions (Araújo & Rozenfeld, 2014; Soberón & Nakamura, 2009). While our findings confirm a high sensitivity of JSDMs to the spatial resolution of the input data, we found equivocal evidence with respect to the hypothesized directed change in species associations. On the one hand, the peak in the relative importance of species associations at 250 m grain size might indicate a stronger role of biotic processes in structuring small-scale community variation, and the higher proportion of significant negative values at finer-grain sizes may reflect a clearer signal of interspecific competition. On the other hand, estimated species associations were generally shifted towards positive values and showed a positive correlation with functional similarity, which does not support the assumption of biotic interactions being more evident in fine-grained community data. Overall, our findings highlight the scale dependence of both community data and models and caution against a naive ecological interpretation of JSDM results.



FIGURE 1 Joint species distribution models species association matrices estimated at different grain sizes (columns) and sampling periods (rows). For better comparison, the order of species is fixed across matrices and was determined by hierarchical clustering (UPGMA) of the species association matrix from $D_{250,5}$, where the relative importance of species associations was highest. Values with high statistical support are outlined in dark grey

Joint species distribution models showed better model fits on coarse-grained data, confirming hypothesis 1 and lending support to the view that stochastic processes (e.g. dispersal and ecological drift) shape community composition locally, whereas deterministic processes (e.g. environmental filtering) dominate at coarser observational scales (Chase, 2014; Chase & Myers, 2011). A further decomposition of the explained variance into fixed (environmental predictors) and random (species associations) effects revealed a peak in the importance of species associations at 250 m grain size, although environmental variables remained more important under all conditions. These results only partially confirm hypothesis 2, in which we stated that the explanatory power of environmental predictors should be highest at coarse-grain sizes, whereas species associations should explain a larger portion of community variation at finer grains. However, the response of species associations with changes in grain size may help identifying the spatial scale of latent abiotic or biotic processes. For example, the grain size at which we observed the highest relative importance of species associations $(250 \times 250 \text{ m}, 6.25 \text{ ha})$ would be consistent with the scale at which habitat structure varies (Pearman, 2002) or competitive interactions play out in avian communities (Dhondt, 2012), but

not necessarily capture the high spatial variability in microclimatic conditions (Chen et al., 1999).

Considering the statistical distribution of species associations allows a further evaluation of potential mechanisms underlying patterns in co-occurrence. Here, the high frequency of positive values contradicts a major role of competition, as this would induce more negative (repulsive) species associations (Araújo & Rozenfeld, 2014). A high proportion of positive species associations among Swiss breeding birds was reported previously by Tobler et al. (2019) and Zurell, Franklin, et al. (2020). Both studies acknowledge that this finding is more likely the result of shared responses to unobserved environmental gradients, for example, habitat preference for forest edge versus forest interior, rather than of strong facilitative interactions among the majority of Swiss bird species. Our multi-scale analysis corroborates this interpretation, as the over-representation of positive associations remained relatively stable across grain sizes, thus rejecting our hypothesis 3 which postulated an increasing proportion of negative associations at smaller grain sizes. Although we found slightly more significant negative associations at smaller grain sizes, this result should be interpreted with caution as it may simply reflect a reduction in parameter uncertainty due to a larger number of sampling units. Finally, the correlation between functional



FIGURE 2 Contrast of species associations estimated at different spatial grain sizes (columns) and sampling periods (rows). Each dot represents a pair of species, with the Y-value denoting the estimated species association at the finest-grain size (125 m) and the X-value denoting the corresponding value at increasingly coarse-grain sizes. Dot colour indicates whether the species association of a given species pair was significant at the fine (orange), coarse (purple), or both grain sizes (black). Dots closer to the identity line indicate more consistent estimates

similarity and species associations, which behaved opposite to the expectations formulated in hypothesis 4, provided further evidence that the signature of biotic interactions is not discernible in the spatial distribution of species in the analysed dataset. These findings align with a number of recent conceptual (Blanchet et al., 2020; Dormann et al., 2018) and empirical (Barner et al., 2018; Mod et al., 2020; Sander et al., 2017) studies highlighting the challenges in inferring biotic interactions from spatial data. In the following, we discuss how these challenges interact with spatial scale and relate to the prevalent modelling frameworks and data types in community modelling.

Wiens (1989) attributed the long-standing debate about the role of competition in structuring animal communities to the "imposition of a single scale on all of the species in the community". JSDMs face a similar problem by requiring a fixed resolution at which communities are defined. Mobile organisms such as birds, however, vary widely in their home range size, territoriality and general prevalence in the landscape (Brown & Orians, 1970). Consequently, no single grain size describes the environmental niches of different species equally well (Chust et al., 2004; Gottschalk et al., 2011). While in classical SDMs the scale of analysis can be somewhat adjusted to the ecology of the target species (Collingham et al. 2000, Chust et al. 2004; Gottschalk et al. 2011), the choice of scale – and, for that matter, also the choice of predictor variables – in JSDMs affects all modelled species differently and induces complex biases in the residual structure of the model. This problem is further exacerbated by the lower rank approximation of species associations in latent variable JSDMs (Pichler & Hartig, 2020; Tobler et al. 2019). The inconsistency of species associations at different grain sizes highlights these complex scaling effects in the residual structure of JSDMs (Figure 2).

Detecting true biotic interactions against the background of these systematic - but unknown - model errors is difficult. Moreover, not only the systematic error in estimated species associations varies with scale but also so does the signature of biotic interactions. In boreal owls, for example, the imprint of negative interactions (interspecific competition and predation) could be detected within a radius of several kilometres (Hakkarainen & Korpimaki, 1996), and facilitative effects mediated through the presence of woodpeckers were demonstrated at even larger scales (Heikkinen et al. 2007). In contrast, other species may exhibit highly localized competition, for example, for nesting sites, but can still co-exist in close proximity (Dhondt and Eyckerman 1980, Dhondt, 2012). Simulation studies suggest that the appropriate scale for detecting biotic interactions depends on the prevalence of the interacting species (Araújo & Rozenfeld, 2014; Zurell et al., 2018). Specifically, Zurell et al. (2018) showed in a simulated community of two species that, depending on



FIGURE 3 Relationship between functional similarity (1-Gower distance) and species associations estimated at different grain sizes (columns) and sampling periods (rows). Mantel correlation is given at the bottom of each plot. Values with high statistical support are outlined in black

the interaction of interest, different levels of prevalence may lead to substantial changes in the magnitude (competition, mutualism) and even direction (predation) of inferred species associations. While we did not analyse the relationship between species' prevalence and species associations specifically, we found higher partial model fits for species that are more prevalent (Figure S1). Considering that differences in abundance and prevalence are a fundamental feature of any realized species assemblage (MacArthur, 1957; Preston, 1962), these findings further challenge the idea of a straightforward link between species associations and biotic interactions.

Finally, a fundamental question regarding the interpretability of JSDM species associations is how reliably biotic interactions can be inferred from typical survey data at all. There is growing evidence that static presence-absence data do not contain enough signal to consistently identify biotic interactions (Barner et al., 2018; Blanchet et al., 2020; Freilich et al., 2018; Sander et al., 2017). This is not unexpected, given the dynamic nature of ecological communities in both space and time. Ecological theory (Lotka, 1926; Volterra, 1926) as well as empirical observations (Gustafsson, 1987; Hakkarainen & Korpimaki, 1996) have demonstrated that the outcome of a biotic interaction (1) varies across time and (2) is reflected more clearly in the relative abundance rather than the presence or absence of species. Our consideration of two sampling periods revealed better model fits and a higher consistency of species associations on long-term data (Table 1, Figure 2), supporting the proposition that temporal information improves the explanatory power of JSDMs (Lany et al., 2018; Schliep et al., 2018). Note, however, that our incorporation of different sampling periods only

affects the number of samples available for fitting an otherwise static JSDM, and consequently does not take full advantage of temporal information in the data. With respect to the beneficial effects of abundance data, however, we were unable to reach any conclusions due to a failure of the models to converge. These convergence problems could indicate that spatiotemporal variation in abundance is influenced by complex demographic and dispersal processes and not easily explained by environmental predictors and species associations alone.

In conclusion, our results highlight several important limitations and potentials for the application of joint species distribution models. First, scale decisions strongly affect the performance of and inference from JSDMs, most likely because in JSDMs both the predictor and the response variables are subject to scaling effects. We therefore recommend considering scale explicitly when modelling communities. This can be achieved either qualitatively, for example, by focusing on species that operate on approximately the same spatial scale, or quantitatively, for example, by using JSDM implementation with spatially structured latent variables (Ovaskainen et al., 2016; Thorson et al., 2015). Second, given their high scale dependence and sensitivity to other confounding factors, species associations cannot be directly interpreted as representation of biotic interactions. Rather, they should serve as a test bed to evaluate if and when independently established biotic interactions create a spatial signal in community data. Finally, even high-quality survey data such as collected by the Swiss monitoring of common breeding birds may lack the spatio-temporal resolution to capture the signal of biotic interactions. Next-generation sampling methods and

computer-aided species identification offer exciting new opportunities to overcome these limitations and produce extremely *dense* ecological datasets (Darras et al., 2019; Ruppert et al., 2019; Willi et al., 2019). The further development of analytical tools should go along with the increasing availability of high-quality data. In particular, we stress the need for more efficient algorithms to fit JSDMs on very large datasets (Pichler & Hartig, 2020; Tikhonov, Duan, et al., 2020) and second the call for JSDM extensions that explicitly take advantage of time-series abundance data (Warton et al., 2015; Zurell et al., 2018).

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DATA AVAILABILITY STATEMENT

Data and code for the reproduction of our results are available for download from the Dryad data repository under https://doi. org/10.5061/dryad.qfttdz0g7.

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BIOSKETCH

Having diverse backgrounds in the fields of macroecology, biogeography and ecological and climatic modelling, the authors share a deep interest in the drivers underlying species distributions and community assembly. The present study arose from a mix of excitement and scepticism regarding the potential of joint species distribution models to extract the signal of biotic interactions from spatial data.

Author contributions: DZ and CK conceived the research question and designed the analysis framework. TS provided data from the Swiss common breeding bird survey and ROW prepared the environmental data. CK conducted the analyses. CK led the writing with significant contributions from all co-authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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