

PRIMARY RESEARCH ARTICLE

Taxonomic and functional homogenization of farmland birds along an urbanization gradient in a tropical megacity

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Abstract

Urbanization is a major driver of land use change and biodiversity decline. While most of the ongoing and future urbanization hotspots are located in the Global South, the impact of urban expansion on agricultural biodiversity and associated functions and services in these regions has widely been neglected. Additionally, most studies assess biodiversity responses at local scale (α -diversity), however, ecosystem functioning is strongly determined by compositional and functional turnover of communities (β -diversity) at regional scales. We investigated taxonomic and functional β -diversity of farmland birds across three seasons on 36 vegetable farms spread along a continuous urbanization gradient in Bangalore, a South Indian megacity. Increasing amount of grey area in the farm surroundings was the dominant driver affecting β -diversity and resulting in taxonomic and functional homogenization of farmland bird communities. Functional diversity losses were higher than expected from species declines (i.e., urbanization acts as an environmental filter), with particular losses of functionally important groups such as insectivores of crop pests. Moreover, urbanization reduced functional redundancy of bird communities, which may further weaken ecosystems resilience to future perturbations. Our study underscores urbanization as a major driver of taxonomic and functional homogenization of species communities in agricultural systems, potentially threatening crucial ecosystem services for food production.

KEYWORDS

agrobiodiversity, Bengaluru, beta-diversity, biotic homogenization, community differentiation, environmental filtering, India, nestedness, turnover, urban agriculture

1 | INTRODUCTION

Urbanization has been identified as one of the main drivers of biodiversity decline and biotic homogenization worldwide (Faeth et al., 2011; McKinney, 2006). The accelerating expansion of urban areas leads to severe land-use changes and can affect biodiversity and

ecosystem functions in persistent ways through habitat degradation or destruction, urban warming and pollution (Grimm et al., 2008; McKinney, 2008). Moreover, cities are growing at an exponential rate with already half of the world population considered as urban dwellers (United Nations, 2018). On top of that, current projections estimate that this number will further increase to reach 68% by 2050

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while most of the ongoing and future urbanization "hotspots" are located in the Global South (e.g., China, India and Sub-Saharan Africa; Bai, 2012; Seto et al., 2012). Cities also offer new opportunities with a growing interest in urban agriculture (Cabannes & Pasquini, 2008; Elmqvist et al., 2013). To date, millions of urban farmers worldwide are producing an estimated 15%–20% of global crops (De Zeeuw et al., 2011; Thebo et al., 2014). On the other hand, urbanization has been identified a major threat to food security in countries with a developing economy as urban sprawl increasingly competes with productive lands (Bai, 2012; Gu et al., 2019).

Consequently, an increasing number of studies have investigated the impact of urbanization on biodiversity and associated ecosystem functions (Grimm et al., 2008; Sol et al., 2020). However, most research focuses on species loss rather than quantifying the wider impact of urbanization on ecosystem functioning (Sol et al., 2020). Additionally, most of these studies are restrained to α -diversity despite the growing body of evidence that β -diversity, that is, the compositional variation among species communities, drives ecosystem functioning across temporal and spatial dimensions (Mori et al., 2018). Taxonomically or functionally distinct communities provide multiple functions, and can complement each other due to community differentiation across space and time (i.e., spatial and temporal turnover) and functional niche differentiation (Mori et al., 2016; Pagani-Núñez et al., 2019; Van Der Plas et al., 2016). However, ecosystem functionality might be impaired if the variation between regional communities is low, as a consequence of biotic homogenization (Hautier et al., 2018; Mori et al., 2018).

A reason for this current lack of understanding may be the many facets of β -diversity, making its interpretation challenging (Anderson et al., 2011; Mori et al., 2018). Indeed overall β -diversity confounds two distinct processes that can be partitioned into additive components, namely turnover (i.e., species replacement among communities) and nestedness (i.e., species loss among communities; Baselga, 2010, 2013). In the context of urbanization, β -diversity typically increases when one or few habitats are disturbed within a region, leading to a local loss of species and an increase in dissimilarity (i.e., nestedness; Socolar et al., 2016). In contrast, such anthropogenic activities can also increase environmental heterogeneity allowing immigration by new species (i.e., species turnover), which further increases β -diversity (Pagani-Núñez et al., 2019).

However, these changes in species composition are not random and some species may be disproportionately affected by urbanization according to their functional or life-history traits (i.e., environmental filtering; Croci et al., 2008; Evans et al., 2011; Sol et al., 2014). Furthermore, not all species contribute equally to ecosystem functioning and the loss of certain functional groups can disrupt crucial ecosystem functions and services (Flynn et al., 2011; Luck et al., 2009). Hence, functional diversity metrics, based on community composition and their associated functional traits, are powerful tools that help quantify how species contribute to ecosystem functioning (Flynn et al., 2011; Hagen et al., 2017; Villéger et al., 2008). In order to investigate whether urbanization homogenizes functional diversity across regional scales, the same β -diversity partitioning

(turnover and nestedness) approach can be used to understand changes in functional β -diversity. Functional β -diversity corresponds to the variation of the multidimensional trait space (i.e., convex hull occupied by a community) among communities (Mori et al., 2018; Villéger & Brosse, 2012). Thereby, functional turnover is driven by functional trait space differentiation (i.e., community differentiation) and functional nestedness occurs when the functional trait space from a community is a subset of another (Villéger & Brosse, 2012; Villéger et al., 2013).

In this study, we focus on birds, one of the best-studied taxa in urban and tropical environments, and with well-established functional traits corresponding to their habitat use, foraging, and behavior (Etard et al., 2020; Tobias & Pigot, 2019). In addition, birds are widespread, conspicuous, and provide essential ecosystem services in tropical agricultural systems, such as pollination and biological pest control (Lee, 2018; Şekercioglu et al., 2016; Whelan et al., 2008). Bird richness is reduced with increasing urbanization intensity, whereas abundance is increased with a peak at intermediate urbanization intensity (e.g., peri-urban area; Batáry et al., 2018). This is due to the dominance of the so-called "urban exploiters", that is, those species with certain functional or life-history traits that are well adapted to urban ecosystems (Evans et al., 2011; Kark et al., 2007; Sol et al., 2014). However, as seen above, species richness and abundance alone does not provide enough information to assess ecosystem functions and services that are rather related to community composition and functional diversity (Flynn et al., 2011; Hagen et al., 2017; Luck et al., 2009). Sol et al. (2020) documented on average 20% decline of functional diversity worldwide in highly urbanized areas compared to surrounding natural habitats. Furthermore, several studies have reported taxonomic and functional homogenization effects of urbanization on avian communities (Devictor et al., 2007; Luck & Smallbone, 2011; Murthy et al., 2016), while ecosystem functioning at regional scales is driven by community differentiation across space and time (Mori et al., 2018; Van Der Plas et al., 2016). It is noteworthy that most studies are still conducted in temperate cities while tropical regions, where most of the current and future urbanization hotspots are situated, remain largely understudied (Chace & Walsh, 2006; Wenzel, A., Graß, I., Raj, V., Nölke, N., Subramanya, S. & Tschardtke, T., unpublished). Additionally, the majority of studies is focusing on categorical urbanization stages (e.g., urban, peri-urban, rural) or contrasting land use types (e.g., natural habitat vs. urban green parks; e.g., Batáry et al., 2018; Hagen et al., 2017; Luck & Smallbone, 2011; Murthy et al., 2016; Sol et al., 2020). Continuous urbanization gradients that are needed to identify non-linear responses and potential thresholds are seldomly studied. Finally, urban agroecosystems have widely been neglected while birds deliver essential ecosystem services for smallholders that are crucial for food security in and around cities of the Global South.

Here, we address these knowledge gaps and study farmland bird taxonomic and functional β -diversity along a continuous urbanization gradient in Bangalore, an Indian megacity. We surveyed birds on 36 vegetable-growing farms along an urbanization gradient of increasing amount of grey area (i.e., sealed surface), thus keeping

local land use constant while systematically varying the landscape context. We repeated our standardized surveys across multiple seasons to account for temporal community turnover. We first aimed at identifying the most important drivers explaining farmland bird taxonomic and functional β -diversity patterns along distinct spatial and environmental gradients. Second, we aimed at investigating the underlying processes (turnover vs. nestedness) that drive the observed β -diversity patterns using distance-decay relationships (i.e., increase in compositional dissimilarity with increasing spatial/environmental distance between sites). We tested two main hypotheses (see Figure 1). In the first hypothesis, β -diversity increases with increasing contrast in urbanization intensity (distance-decay relationship), resulting from an increase of taxonomic and functional turnover, thus leading to greater community differentiation where new species (i.e. urban specialists) substitute species from rural areas (i.e. turnover). In the second hypothesis, β -diversity also increases with greater contrast in urbanization intensity, but this time resulting from species and functional trait loss (i.e., nestedness). Hence, urban communities would represent an impoverished subset of rural communities, as would follow from homogenization of farmland bird communities

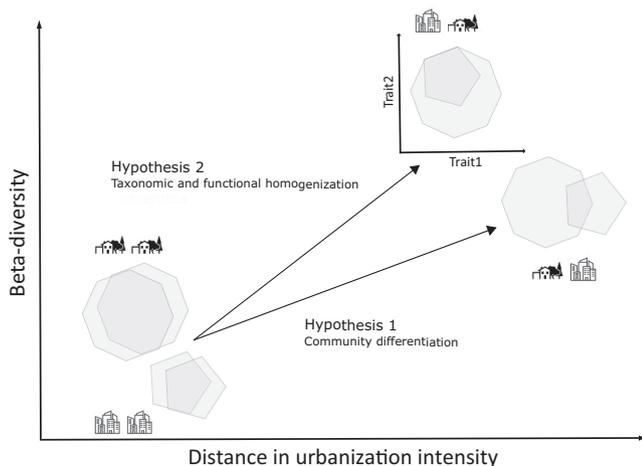


FIGURE 1 Conceptual representation of our hypotheses. The x-axis represents the increasing difference in urbanization intensity between pair of sites (depicted by icons). In our study, this corresponds to the increasing between-site differences in proportion of grey area. The y-axis corresponds to pairwise β -diversity, that is, increasing compositional (taxonomic/functional) differences between communities. The polygons represent the convex hull volume occupied by a community in a multidimensional functional space (here displayed in two dimensions for trait 1 and trait 2). The penta- and octagons represent the functional trait spaces of urban and rural communities respectively. β -diversity increases with increasing distance in urbanization intensity (distance-decay relationship) in both hypotheses but this increase results from two different processes. In Hypothesis 1, it results from an increase of species and functional turnover, leading to greater community differentiation where new species (i.e., urban specialists) substitute species from rural areas. By contrast in Hypothesis 2, increases in β -diversity result from species and functional trait loss (i.e., nestedness), and hence urban communities represent an impoverished subset of rural communities (i.e., homogenization)

with urbanization. Next, we tested whether urbanization is acting as an environmental filter (i.e., higher functional diversity losses than expected by chance given the number of species), using functional diversity metrics combined with a null model approach. Lastly, we simulated species extinctions to assess the impact of species loss on functional richness (i.e., functional redundancy).

2 | METHODS

2.1 | Study area

This study was conducted in Bengaluru (formerly Bangalore), the capital city of the South Indian state of Karnataka (Figure 2). With its 9.6 million inhabitants and a population growth of 8% (Karnataka District Census, 2011), Bengaluru is considered to be one of the fastest growing cities in India (Sudhira & Ramachandra, 2007). Additionally, the city's direct surroundings harbor an ancient agricultural landscape composed by a mosaic of small-scale farms and semi-natural habitats such as trees rows, shrubs, hedges and permanent fallow. The rapid urban expansion, both from the city's edge and around rural villages, increasingly competes with these agricultural and semi-natural lands.

Situated on the Deccan Plateau at an elevation of 920 m above sea level, Bengaluru experiences a moderate tropical climate with three distinct seasons: winter (October–January, the post-monsoon season), summer (February–May, the dry season) and monsoon (June–September).

2.2 | Study design

Our study farms were located along two transects starting in urban Bengaluru. Both transects extended toward rural villages, thus forming a rural–urban gradient in the north and south of the city (Figure 2). Along this gradient, a total of 36 vegetable-producing smallholder farms of similar management intensity were carefully selected as study sites (18 within the north transect and 18 within the south transect). Authorizations to work on the farms were granted by the owners before the start of the fieldwork. In order to account for local urbanization effects (i.e., expansion of rural villages and polycentricity), all sites were selected by pairs (18 pairs in total) of contrasting amount of built-up area in their surroundings (“high” vs. “low” amount of built-up area). We kept a minimum distance of 1 km between two sites to guarantee site independence. Prior analyses showed no effect of neither pair id, nor transect id on our response variables. A land cover map with 10-m spatial resolution was produced from a cloud-free Sentinel-2 L1C imagery that was acquired in November 2016 and preprocessed to L2A data, which were atmospherically corrected. A pixel-wise image classification was performed using a simple deep learning model, a so-called multilayer perceptron network (Awuah et al., 2018). We used this land cover map to calculate the proportional share of grey area (impervious and sealed surfaces, such

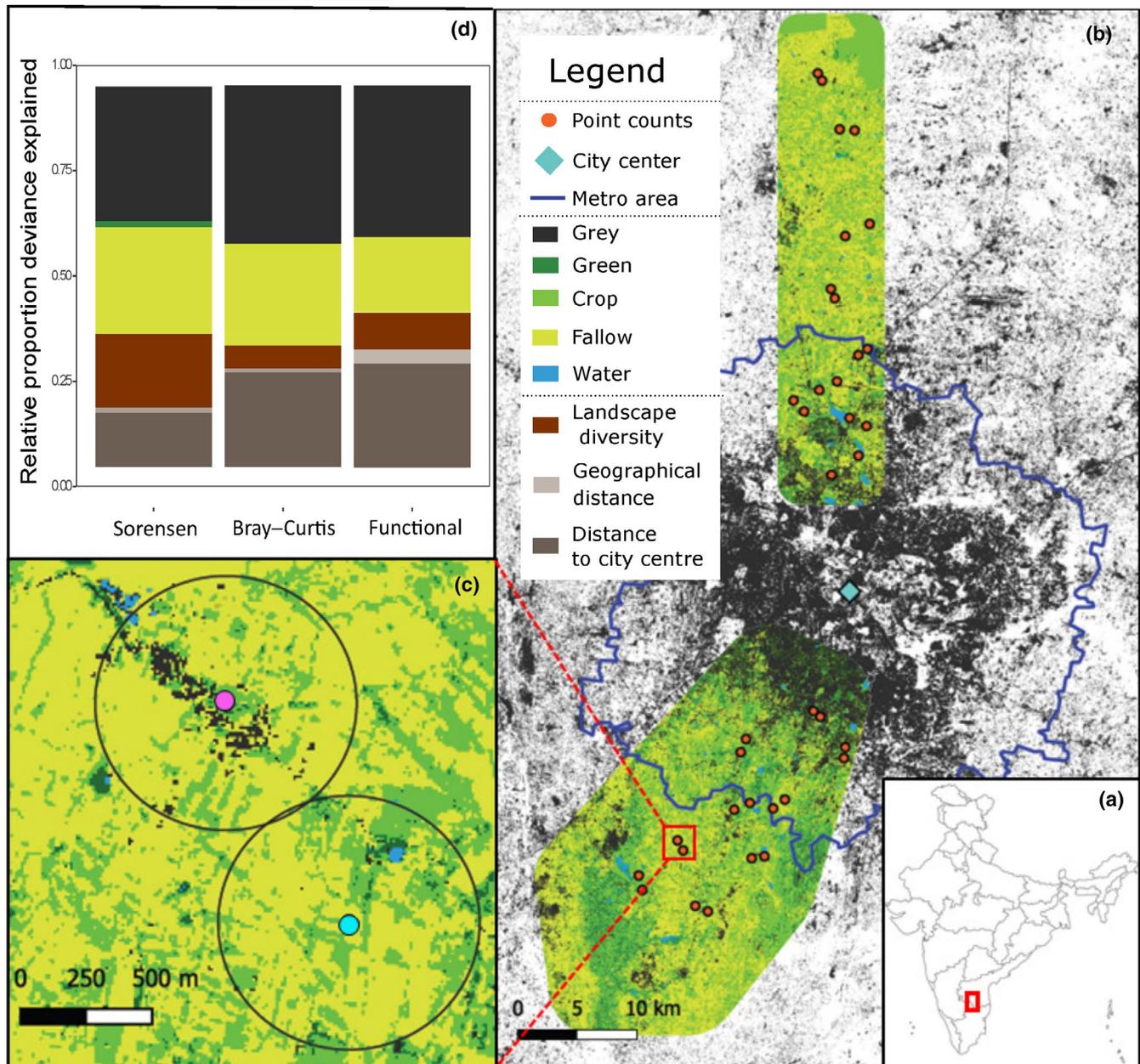


FIGURE 2 Study area. Map of India with the red box highlighting the study region (a). The two transects running north and south from Bangalore with the study sites (b). Example of two locally paired study sites according to their amount (low vs. high) of built-up (grey) area (c). Results from Generalized Dissimilarity Models (see Section 2.4) showing the relative contribution of each predictor (spatial and environmental) to the total explained deviance (goodness of the model fit) (d). We see that grey area is the predictor that explains the highest proportion of the deviance for all dissimilarity measures

as roads, buildings and constructions in general), green area (woody vegetation, such as forest, hedges, tall shrubs or eucalyptus plantations) and fallows (uncropped fields and margins, usually with some herbaceous vegetation) as well as the landscape diversity (Simpson's diversity index) within a buffer of 500-m radius around the 36 farms (see Data S1 for details). Birds were surveyed in each site twice per season (six survey rounds in total, $N = 216$) using standardized point counts. Every bird seen or heard during a period of 15 min within a fixed 50-m radius from the center of the farm was recorded. Bird surveys took place under good weather conditions (low wind, light rain) and only in early morning hours (from 6:00 to 8:00 AM) when the

birds' activity was highest. A single observer (Varsha Raj), who has an expert knowledge of the local avifauna (and more than 12 years of experience), conducted the entire bird census. Data were collected between the September 1, 2017 and the May 30, 2018. Flyovers and strictly aquatic birds were excluded from analyses.

2.3 | β -diversity metrics

We used pairwise Sørensen (incidence-based—unshared species between communities), Bray-Curtis (abundance-based—unshared

individuals between communities) and functional (incidence-based—unshared functional trait space between communities) dissimilarities. Sørensen dissimilarity (β_{SOR}) represents total β -diversity and can be partitioned into two additive components, namely species turnover or β_{sim} (i.e., species replacement among communities) and nestedness or β_{sne} (i.e., species loss among communities; Baselga, 2010). Similarly, the Bray–Curtis index (d_{BC}) can be decomposed into two additive components, accounting for a balanced variation in abundance or $d_{\text{BC-bal}}$ (i.e., individuals replacement or turnover) and an abundance gradient or $d_{\text{BC-gra}}$ (i.e., individuals loss or nestedness; Baselga, 2013). Functional dissimilarity ($\beta_{\text{func.sor}}$) was calculated as the unshared functional richness (i.e., based on the intersection of the convex hulls in the multidimensional functional traits space) among communities. It is derived from the Sørensen index and is thus partitioned in the same way with functional trait space replacement (i.e., functional turnover or $\beta_{\text{func.sim}}$) and functional trait space loss (i.e., functional nestedness or $\beta_{\text{func.sne}}$) between sites (Villéger et al., 2013). To calculate functional dissimilarity, we selected 14 traits characterizing each bird species diet and foraging strata as well as mean body mass obtained from the EltonTraits database (Wilman et al., 2014). We restrained our analysis to traits describing dietary and foraging niches, and excluded morphological traits (except body mass, which is related to energetic constraints, competitive ability and pace of life, thus indirectly to resource use; see Cannon et al., 2019; Greenberg et al., 1995). These chosen traits directly relate to the birds' resource utilization and are good indicators of their functional roles in ecosystems (Cannon et al., 2019; Hagen et al., 2017; Petchey & Gaston, 2006; Philpott et al., 2009; Sol et al., 2020). For instance, insectivorous birds are likely contributing to pest control, frugivorous birds to seed dispersal, nectar feeders to pollination and scavengers to carrion removal. The strata where the birds forage is also expected to play an important role; for example, influence their ability to capture insects in agroecosystems (Philpott et al., 2009). We classified all species in feeding guilds according to their preferred food resource (seed, fruit, nectar, other plant material, invertebrate, vertebrate, scavenge, omnivore) and characterized their foraging behavior according to their optimal foraging strata (ground, understory, medium, canopy, aerial; see Table S6). These traits were thus treated as categorical variables (Montaño-Centellas et al., 2021). As diet and foraging strata are categorical variables whereas body mass is a continuous variable, we first built a species-by-species Gower's distance matrix, which allows for different types of variables to be mixed (Gower, 1971). We calculated Gower's distances with the function "gawdis", which gives equal weight to each trait (de Bello et al., 2021). We then ran a Principal Coordinate Analysis (PCoA) on this distance matrix to summarize the trait data. Following a trade-off between computation time and information quality (parallelization on High Performance Computing Cluster was not working beyond four axes; Villéger et al., 2013) we kept the first four PCoA axes as synthetic traits to calculate and partition functional dissimilarity. Nevertheless, the functional trait space defined by these four PCoA axes gives an accurate representation of the functional distances between species (Mantel test between Gower's

distances and Euclidean distances in the four-dimensional convex hull composed of the four PCoA axes: $r = 0.92$; $p < 0.001$). All indices were calculated using the *betapart* R-package (Baselga et al., 2018).

2.4 | Statistical analyses

Data were aggregated per site and pooled either by season or for the entire year ($N = 36$). All statistical models were systematically carried out for the three seasons separately (i.e., winter, summer, and monsoon) and for the three seasons pooled together. All statistical analyses were conducted in R version 4.0.2 (R Core Team, 2020).

First, we aimed at identifying the most important predictor, which explains β -diversity patterns along the urbanization gradient. We used Generalized Dissimilarity Modelling (GDM; Ferrier et al., 2007), a matrix regression technique that allows the relation between compositional dissimilarity and spatial or environmental gradient to be non-linear. Additionally, it has the advantage of being non-stationary and depicts the rate of compositional variation at any point along a given gradient. This is achieved due to the use of monotonically increasing flexible *l*-spline functions (partial regressions) fitted for each predictor (Ferrier et al., 2007). When plotted, the maximum height of the *l*-splines depicts the magnitude of a given predictor's effect on β -diversity (partial ecological distance), while holding all the other predictors constant, and the slope of the curve indicates the rate of compositional change at any point along the gradient. When the *l*-splines' coefficients of a predictor are summed, it indicates its importance in driving β -diversity (which also corresponds to the maximum height of the curve). Using the "gdm" function from *gdm* R-package (Fitzpatrick et al., 2020) we fitted full GDMs with all our environmental (i.e., proportional share of grey, green, and fallow area and landscape diversity) and spatial (pairwise geographical distance and orthogonal distance from the city center) predictors with taxonomic (Sørensen and Bray–Curtis index) and functional β -diversity as response variables. These models were fitted with the default of three *l*-spline basis functions per predictor. We calculated significance of each predictor using Monte Carlo permutation with stepwise backward selection ("gdm.varImp" function). We additionally fitted GDMs with our predictors individually and then partitioned their explained deviances (goodness of the model fit) to measure their relative contribution in explaining β -diversity (Fitzpatrick et al., 2013; König et al., 2017). Finally, we calculated the uncertainty for the GDM plots (i.e., standard deviation) using the function "plotUncertainty" with 100 bootstrap iterations on a subsample representing 30% of plot pairs for each model (Gossner et al., 2016).

Second, in order to answer our two main hypotheses (see Figure 1), we investigated the underlying processes (turnover vs. nestedness) that drive both taxonomic and functional β -diversity. Using the *betapart* R-package (Baselga et al., 2018), we partitioned the respective total β -diversity into its turnover and nestedness components. We calculated the pairwise dissimilarity between all sites ("(funct.)beta.pair") to observe the distance-decay relationships

between all β -diversity metrics and environmental distances between sites. Distance-decay relationship (here the increase of compositional dissimilarity with increasing environmental distance between sites) is one of the most used method to analyze the rate of compositional changes in function of spatial or environmental distances (Nekola & White, 1999). Baselga (2010, 2013) suggested to use this method to investigate which process (turnover vs. nestedness) drives the observed β -diversity patterns. We fitted negative exponential distance-decay models ("decay.model") with taxonomic (Sørensen and Bray–Curtis index) and functional β -diversity, as well as their turnover and nestedness components, as response variables and the distance in grey area proportion between all possible site pairs—the most important predictor identified with GDMs—as explanatory variable. The use of negative exponential distance-decay models (compared to other linear models) meets the assumption of asymptotic increase of dissimilarity constraints between 0 and 1 (Baselga, 2013). We additionally fitted decay models with β -diversity metrics calculated for different feeding guilds (i.e., invertebrates, fruits, seeds, omnivores) categorized based on the EltonTraits database (Wilman et al., 2014). These models adjust a GLM (with a log link function and a Gaussian error distribution) to incorporate a dissimilarity matrix as response variable. They compute a pseudo- R^2 (goodness of model fit) and a p -value by randomizing 1000 times predictions and calculating the number of times the model deviance was smaller than the randomized deviance (Gómez-Rodríguez & Baselga, 2018). We finally assessed whether intercepts and slopes of different β -diversity metrics differed by bootstrapping 1000 times the coefficients ("boot.coefs.decay"). p values were then calculated based on the proportion of bootstrapped values larger or smaller from each other (Gómez-Rodríguez & Baselga, 2018).

To provide robust evidences that the observed functional β -diversity patterns were the result of environmental filtering, we calculated three commonly used and well-established functional diversity indices with the FD R-package (Laliberté et al., 2015; Moullot et al., 2013). Using the same traits (four PCoA axes) as for the computation of functional β -diversity, we calculated functional richness, functional dispersion and functional evenness (Laliberté & Legendre, 2010; Villéger et al., 2008). Functional richness (or FRic) represents the multidimensional functional trait space occupied by a community (i.e., convex hull volume). It can be correlated with species richness since the more species there are, the larger the convex hull volume likely becomes. Functional dispersion (or FDis) represents the mean functional distance of each species from a community to the centroid of all species of this community and is abundance weighted. Functional evenness (or FEve) measures how regular functional traits are distributed within the functional space occupied by a species community and is abundance weighted too. If urbanization is acting as an environmental filter, functional diversity metrics from the observed communities should differ from that of randomly assembled communities. We thus implemented a null models approach where we assembled 1000 randomized communities by re-shuffling species while maintaining species richness and abundance constant, using the "independent-swap" algorithm from *vegan* R-package (García-Navas et al., 2020; Gotelli & Entsminger,

2001; Oksanen et al., 2017). We then calculated the Standardized Effect Size (SES) of the three functional diversity indices as followed: $(\text{Obs-FD} - \text{mean}(\text{Rand-FD}))/\text{sd}(\text{Rand-FD})$. When SES is ± 1.96 (corresponding to the 95% CI) it indicates that our observed values are significantly higher or lower (i.e., environmental filtering) than expected by chance under a null model. To further interpret the impact of species loss on functional richness, we calculated the functional redundancy (FR) based on simulations of random species extinction following Teichert et al. (2017), by sequentially removing species and recalculating functional richness (convex hull volume in the multidimensional functional trait space; Teichert et al., 2017). We then calculated the Area Under the Curve (AUC) defined as the proportion of functional richness loss against that of species richness. Smaller AUC values indicate faster decay of functional richness with species extinctions, that is, lower functional redundancy. AUC values were averaged over 100 iterations for each community. Lastly, we fitted generalized linear models with our functional diversity indices, their standardized effect size, and functional redundancy as response variables and the proportional share of grey area (best predictor to explain β -diversity along the urbanization gradient) as explanatory variable. Grey area was log-transformed as it was not normally distributed and scaled for better model convergence. FRic and FEve (both constraint between 0 and 1) were fitted with a beta distribution (*betareg* R-package; Cribari-Neto & Zeileis, 2010). As FDis is not naturally constraint between 0 and 1, we first applied a correction by dividing FDis of each site by the maximum FDis value of all sites before fitting the "betareg" model. SES_{FRic} , SES_{FDis} , SES_{FEve} , and FR were fitted with a Gaussian error distribution. All models were validated using diagnostic plots.

3 | RESULTS

Across all seasons, we recorded 11,000 terrestrial birds from 126 species (50 families; see Table S6). We estimated species richness using Chao 1 estimator, which indicated that we sampled 82.4% of the overall regional farmland bird richness (Chao, 1987).

3.1 | β -diversity patterns along the urbanization gradient

β -diversity patterns were only significantly affected by two predictors: The amount of grey area within a buffer of 500 m and the geographical distance between sites respectively (Table S1). However, when we summed the three l -splines' coefficients of each predictor, grey area had the largest effect on both taxonomic (Sørensen and Bray–Curtis) and functional β -diversity. Furthermore, partitioning the explained deviance yielded the same result with grey area being the predictor that contributed the most to explaining the variance in Sørensen (41%), Bray–Curtis (35%) and functional (42%) dissimilarities (Figure 2d; Table S2). These results demonstrate that grey area is the most important predictor to explain β -diversity

patterns along the urbanization gradient. However, the rate of compositional change differed between the three β -diversity metrics (Figure 3). Bray–Curtis presented a general trend for a saturating response with the curve bending already with a small increase in grey area. This suggests that most of the compositional changes in species abundance/dominance already occurred in little-urbanized areas, whereas Sørensen exhibited a linear response. In contrast, functional dissimilarity showed an accelerating response, indicating that more compositional variations occurred at the end of the gradient, that is, at higher urbanization intensity. These patterns slightly differed across the three seasons with a higher taxonomic

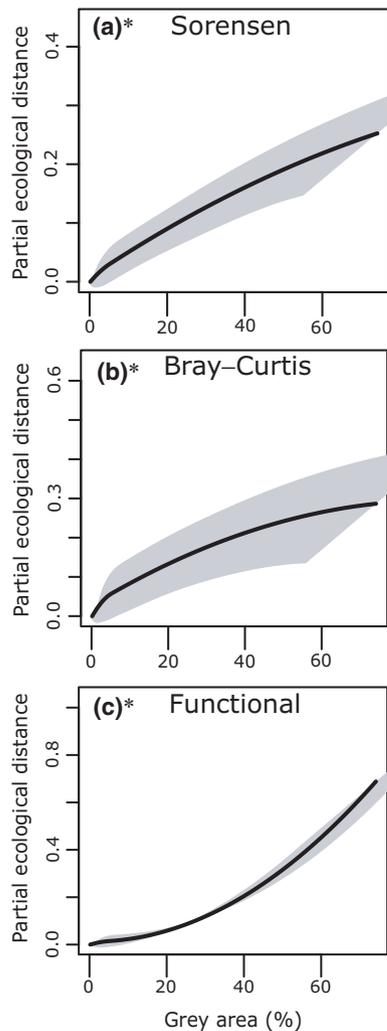


FIGURE 3 β -diversity patterns along the grey area gradient (best predictor). The plots show the Generalized Dissimilarity Models' (GDM) fitted I -splines (partial regression) corresponding to the magnitude of the effect (partial ecological distance) of grey area on Sørensen (a), Bray–Curtis (b) and functional (c) dissimilarities, holding all the other predictors constant. The lines represent model predictions and the grey belts depict uncertainty. The maximum height of each curve indicates the magnitude of the effect on β -diversity (total amount of compositional change) associated with grey area and the shape of the curves indicates the rate of compositional change along the gradient. Significance level: * $p < 0.05$

and functional dissimilarity in winter, which exhibited, in general, a linear trend. A different pattern was observed during the summer and the monsoon seasons with a saturating response for Sørensen and Bray–Curtis dissimilarities, and an accelerating response for functional dissimilarity; that is, again indicating more variations at the end of the gradient (see Figure S1).

3.2 | Underlying processes that drive the observed β -diversity patterns

With increasing environmental distance between sites (i.e., contrasting proportions of grey area) the overall dissimilarity between communities was increasing for both taxonomic (Sørensen and Bray–Curtis) and functional β -diversity (Table S3; Figure 4). However, when β -diversity was partitioned, the two β -diversity components exhibited different patterns. The distance-decay of species turnover (β_{sim}) was negative indicating taxonomic homogenization whereas it was positive for individuals turnover (d_{BC-bal}) and constant for functional turnover ($\beta_{func.sim}$). While the nestedness component of the Bray–Curtis index (d_{BC-gra}) remained constant, it strongly increased with increasing grey area distance between sites for both Sørensen (β_{sne}) and functional dissimilarities ($\beta_{func.sne}$), suggesting that urban communities are a subset of rural ones, both in term of species composition and functional trait space. These results indicate that while abundance-based β -diversity (Bray–Curtis) is driven by individuals turnover (i.e., balanced variations), both species-based (Sørensen) and functional β -diversity are driven by loss of species or functional trait space.

Regarding decay models of different feeding guilds, we found distinct patterns in relation to dietary requirements (Figure 4, smaller panels). Overall β -diversity (β_{sor} and d_{BC}) again increased with increasing distance in grey area between sites for all feeding guilds. We found higher intercepts and steeper slopes for invertebrate- and seed-eating species (bootstrapped $p < 0.001$). However, while the distance-decay of species turnover (β_{sim}) was negative for omnivorous, frugivorous and birds feeding on invertebrate, it was positive for granivorous birds, thus indicating a turnover of seed-eating species from rural to urban areas. For abundance-based turnover (d_{BC-bal}) both granivorous and omnivorous birds had a positive distance-decay relationship, while it was constant for frugivorous species and negative for birds feeding on invertebrate. The distance-decay of nestedness increased for both Sørensen (β_{sne}) and Bray–Curtis (d_{BC-gra}) index with invertebrate feeding birds having the steeper slope (bootstrapped $p < 0.001$). Our results suggest that birds feeding on invertebrate were the most negatively affected in terms of species loss due to increased nestedness of communities while omnivorous and granivorous species exhibited a greater turnover. As overall findings across pooled seasons did not differ from individual seasons, we decided to emphasize the results from the pooled data. Analyses and results related to the three separate seasons are available in supporting material (Table S4; Figure S2).

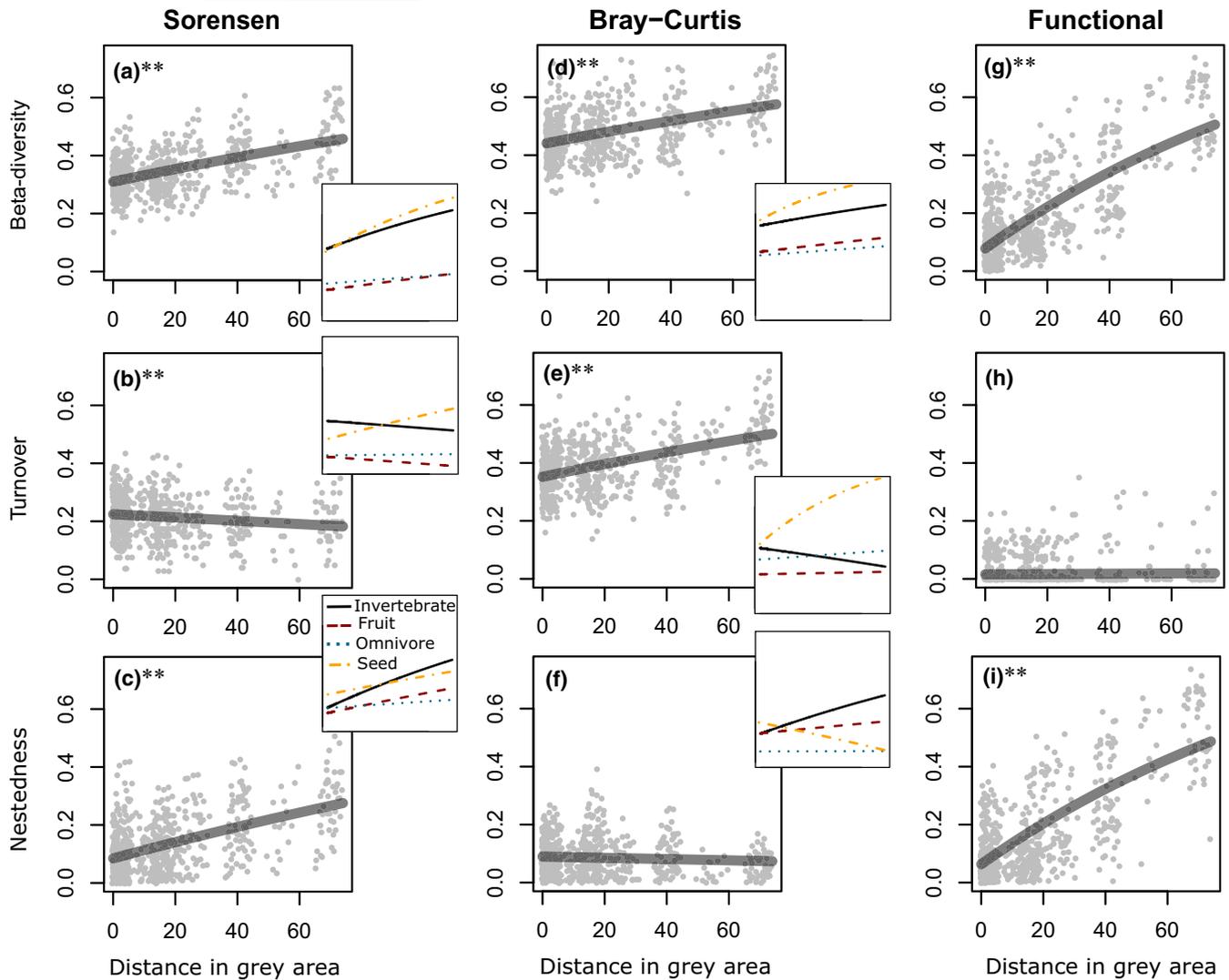


FIGURE 4 Underlying processes that drive the observed β -diversity patterns. The plots show distance -decay relationships between Sørensen (a), Bray-Curtis (b) and functional (c) dissimilarities and their turnover and nestedness components [(d)–(i)] and increasing environmental distance between sites with different proportion of grey area. These relationships indicate whether the increase of total β -diversity is driven by species/functional traits space replacement (i.e., turnover) or species/functional traits space loss (i.e., nestedness). The lines represent decay models' (adjusted GLM) predictions and the grey dots depict all pairwise comparisons. The insets (smaller panels) present the results for four different feeding guilds (invertebrate: plain black line; fruit: dashed red line; omnivore: dotted blue line; seed: orange dash-dotted line). Significance levels: ** $p < 0.01$, * $p < 0.05$

3.3 | Functional diversity

Grey area had a negative effect on functional richness (FRic) and functional dispersion (FDIs; Figure 5; Table S5) indicating losses of functional trait space and reductions of the mean distances between species (i.e., reductions in trait dissimilarity), thus suggesting that farmland bird communities tend to become more functionally similar (clustered) with increasing grey area. Functional evenness (FEve) positively increased with increasing grey area indicating that the distance between species along the minimum spanning tree was more regular with increasing grey area. In addition, the standardized effect size of functional dispersion SES_{FDIs} and functional evenness SES_{FEve} presented lower values (± 1.96) than expected by chance given the species richness (Figure S3; Table S5), indicating

that farmland bird communities were not randomly assembled but filtered in function of their functional traits. Lastly, functional redundancy (calculated as the AUC defined as the proportion of functional richness loss along random species extinction sequences) also significantly decreased with increasing grey area (Figure 5; Table S5), implying that urban communities are more sensitive to species loss.

4 | DISCUSSION

We found that the amount of grey area in the landscape was the best predictor to explain both taxonomic and functional β -diversity of farmland bird communities. Partitioning β -diversity

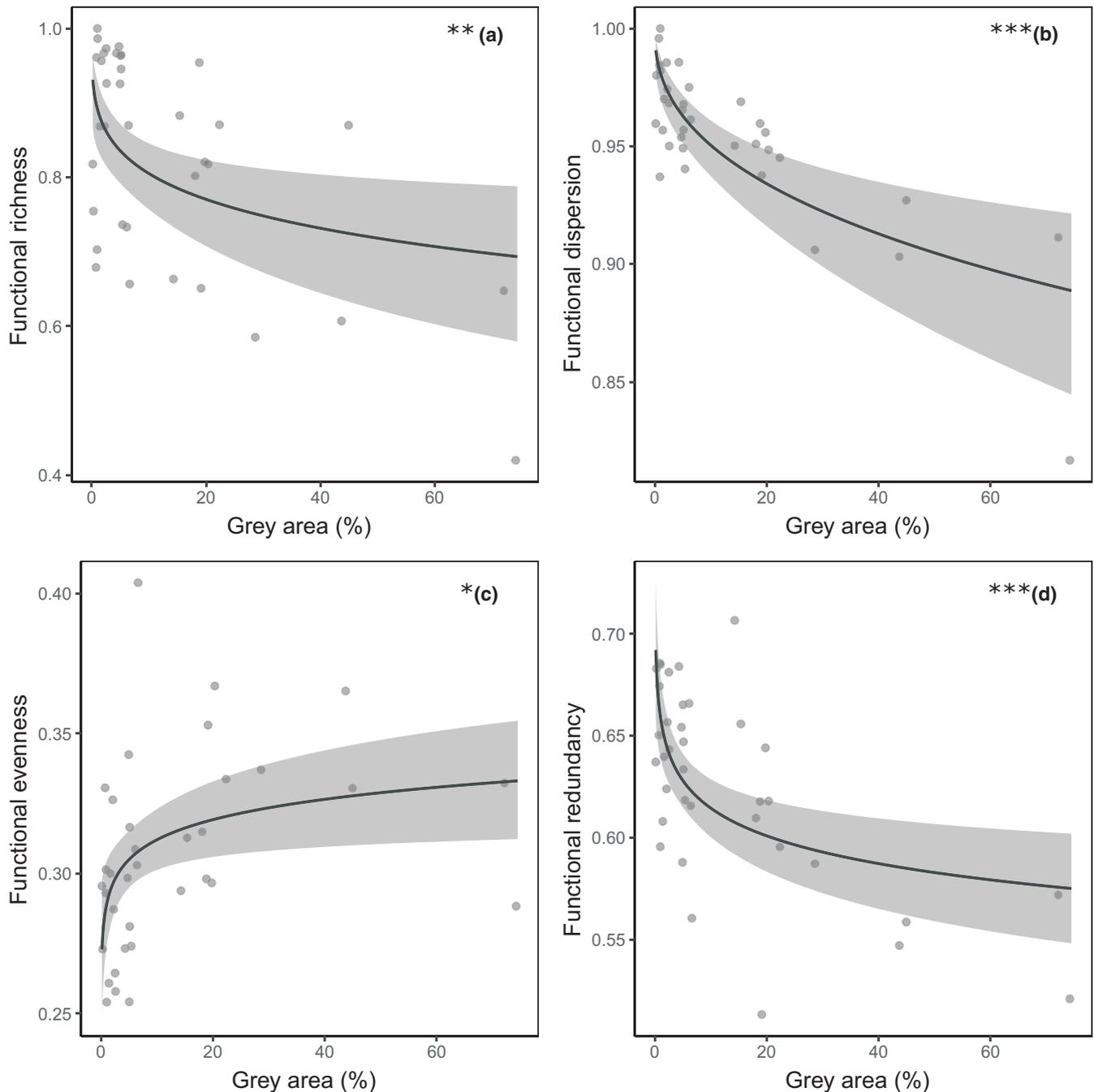


FIGURE 5 Urbanization acting as an environmental filter. Functional richness (a), functional dispersion (b), functional evenness (c) and functional redundancy (d) are affected by the amount of grey area (log) within a 500 m radius buffer. The lines and the grey belts represent model predictions and 95% confidence interval, the points depict raw data. The x-axes (grey area) were back-transformed for plotting. Significance level: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

revealed that these compositional changes were driven by species and functional trait loss, while urban tolerant birds became increasingly dominant with increasing between-sites difference in the proportion of grey area. Overall, these results support our second hypothesis that taxonomic and functional homogenization of farmland bird communities along the urbanization gradient is driven by loss of species and functional traits (e.g., insectivores). Increasing nestedness in terms of species incidence-based

(Sørensen) and functional β -diversity indicates that urban communities represent an impoverished subset of rural communities. Functional diversity losses were higher than expected by chance given the number of species, thus demonstrating that urbanization acts as an environmental filter. Moreover, these urban communities had lower functional redundancy, thereby making the ecosystem functions they deliver more vulnerable in the face of future urbanization.

4.1 | Grey area predominantly drives taxonomic and functional β -diversity

Using Generalized Dissimilarity Modelling (GDM), we first found that grey area was the best predictor to explain both taxonomic and functional β -diversity patterns along the urbanization gradient (Figures 2d and 3; Tables S1 and S2). Although urban areas are a complex mosaic of different land uses and environmental stressors (e.g., light and noise pollution, urban warming, human activities; see for examples Arroyo-Solís et al., 2013; Da Silva et al., 2015), which we did not quantify, grey area (also called built-up or impervious area) has widely been used in many studies as a proxy to assess the effects of urbanization across many taxa (Buchholz & Egerer, 2020; Geslin et al., 2016; Knop, 2016; Piano, Bona, et al., 2020; Piano, Souffreau, et al., 2020; Planillo et al., 2021). Our findings are also congruent with other studies which demonstrated the importance of built-up area in driving α - (Wenzel et al., unpublished) and β -diversity (Meffert & Dziock, 2013) of bird communities both in the tropics and in temperate regions. However, the effects of grey area on compositional changes were not linear, as already observed in other studies (Fitzpatrick et al., 2013). Abundance-weighted β -diversity (Bray–Curtis dissimilarity) showed a saturating response, suggesting that most of the compositional changes in species abundance/dominance already occurred in little-urbanized areas (Figure 3). This contrasts with studies that found a peak in bird abundance at intermediate levels of urbanization (e.g., suburban areas; see Batáry et al., 2018). The relationship with Sørensen dissimilarity was more linear, indicating that changes in species composition were constant (of same magnitude) along the whole urbanization gradient, from rural to highly built-up areas (Figure 3). In contrast, functional β -diversity showed an accelerating response along the grey area gradient, which suggests a strong variation in functional composition, especially at the end of the gradient (i.e., highly built-up areas; Figure 3). These spatial patterns were consistent across the summer and the monsoon seasons, but not during winter (Figure S1), where the higher dissimilarity may result from an increased number of overwintering visitors. Indeed, it has been demonstrated that urban tolerance changes through the year with different patterns for migratory and breeding/resident species (Callaghan et al., 2021).

4.2 | Underlying processes that drive the observed β -diversity patterns

To unravel the underlying processes that drive the observed patterns, that is, species loss versus species turnover, we partitioned β -diversity into its nestedness and turnover components (following Baselga, 2010, 2013). Partitioning incidence-based (Sørensen) β -diversity revealed that taxonomic composition changes were mostly driven by the nestedness component whereas the distance-decay of species turnover with increasing distance in grey area was negative (Figure 4). These findings indicate loss of species between sites with increasing grey area distance. However, compared to other studies (Hagen et al., 2017; Sattler et al., 2011), except for granivorous birds,

species removed from rural areas were not replaced by new species (e.g., urban specialists) and overall urban communities were thus a subset of rural communities instead of being distinct. Focusing closer on granivorous birds, we discovered that they were mostly represented by members of the *Columbidae* family, whose abundance increased with increasing grey area in the landscape (Figure S4). In contrast, abundance-based β -diversity (Bray–Curtis) was driven by its turnover component (Figure 4), suggesting increasing dominance of few species (Evans et al., 2011; Sol et al., 2020). These were urban-tolerant species belonging to the *Columbidae*, *Sturnidae* and *Corvidae* families (see Figure S4), which have been previously identified as urban exploiters (Evans et al., 2011; Sol et al., 2014). In addition, those species remaining in urban areas were functionally similar, representing an impoverished subset of rural communities. Indeed, functional β -diversity was also driven by its nestedness components with almost no functional turnover (Figure 4), which shows that the observed species turnover (Sørensen) is due to the substitution of species with similar functional traits. This indicates that β -diversity is not driven by niche differentiation but by taxonomic and functional homogenization, hence supporting our second hypothesis (see Figure 1). It should be noted that the observed abundance turnover (Bray–Curtis) may imply that abundant species in urban areas have different traits than abundant species in rural areas through shift in species dominance as suggested in Figure S4.

4.3 | Urbanization as an environmental filter of farmland bird communities

We further estimated the effect of grey area on three functional diversity indices and their standardized effect sizes (SES) to provide more robust evidence that the observed functional homogenization of communities reflects environmental filtering. We found that both functional richness and functional dispersion (Figure 5; Table S5) were negatively affected by an increase of grey area. Furthermore, the standardized effect size of functional dispersion (Figure S3) was lower at the end of the gradient than expected by chance given the number of species (i.e., underdispersed), supporting evidence of environmental filtering in sites with a high amount of grey area (i.e., intensively urbanized areas). This finding is in line with other studies, for instance Sol et al. (2020), who documented a worldwide decline of 20% of birds' functional diversity in highly urbanized environments compared to the surrounding natural habitats, or Schütz and Schulze (2015), who found a decrease of functional diversity with an increasing amount of grey area around urban parks in Vienna. In addition, the standardized effect size of functional evenness (SES_{FEve}) was overdispersed in low built-up areas and underdispersed in highly built-up areas. This would suggest an under-utilization of the niche space (e.g., food resources) in urban environment (Mason et al., 2005), presumably mediated by the decline of certain feeding guilds (e.g., insectivorous birds). This could result from a similar mechanism described by Pagani-Núñez et al. (2019): they compared bird assemblages between natural, rural and urban areas in south and

southwest China and reported no change in niche overlap (i.e., no niche over-utilization), but increasing niche width from natural to urban areas; that is, urban tolerant species use empty niches from lost species (niche under-utilization; Pagani-Núñez et al., 2019). In addition, some functional traits were disproportionately affected by urbanization (Crocì et al., 2008; Evans et al., 2011). Indeed, insectivorous birds showed stronger losses with increasing grey area than other feeding guilds (Figure 4). This is in line with other studies that found evidence of environmental filtering for particular traits, such as insectivorous birds typically more affected by urbanization than granivorous or omnivorous species (Callaghan et al., 2020; Jokimäki et al., 2016; Máthé & Batáry, 2015). In contrast, omnivorous species, such as *Corvidae* and *Sturnidae* usually benefit from urbanization (Devictor et al., 2007; Evans et al., 2011; Sol et al., 2014; Callaghan et al., 2019 and see also Figure S4).

4.4 | Urban communities are more sensitive to species loss due to lower functional redundancy

Functional redundancy decreased with increasing grey area (Figure 5; Table S5), thus indicating that urban communities are more sensitive to species loss than rural assemblages in regard of the functions they can provide. This result may first seem contradictory given the fact that we found urban communities to be functionally more similar. Nevertheless, since urban communities are functional subsets of rural ones, there are fewer species remaining in urban areas that deliver similar functions (see also Sol et al., 2020). Indeed, although on average more functionally similar than those of rural communities, species remaining in urban habitat (urban tolerant) can still exhibit different functions (e.g., seed-eating sparrows vs. omnivorous crows) because species with similar traits (e.g., seed-eating sparrows vs. seed-eating larks) can differ in their response to urbanization (Flynn et al., 2009). By contrast, rural assemblages often have higher species and functional richness because of higher species turnover so that multiple species can share similar functions, which increases functional redundancy (Villéger et al., 2012). The linear relationship between species and functional richness further suggests that each species can add specific functional trait expressions (Figure S5), and that a high diversity is needed to maintain ecosystem functioning (Isbell et al., 2011).

4.5 | Potential implications for ecosystem services

Urbanization is a driver of biodiversity loss across many taxa and homogenizes biological communities, risking impairing ecosystem resilience (Devictor et al., 2007; Knop, 2016; Luck & Smallbone, 2011; Piano, Souffreau, et al., 2020). The taxonomic and functional homogenization of bird communities and the decline of avian functional diversity could thereby disrupt important ecological functions and services in urban ecosystems (Sol et al., 2020). Moreover, the decrease of functional redundancy (species delivering similar functions,

see Figure 5), which is often considered as an insurance against future species loss, may further weaken ecosystem resilience to future perturbations. However, we did not quantify ecosystem functioning and further investigations are required to relate biotic homogenization and loss of functional diversity to the delivery of ecosystem services and human well-being in cities (Díaz et al., 2011). Nevertheless, it has been demonstrated that birds provide important services in urban environment such as biological pest control, seed dispersal, pollination and carrion removal (e.g., see Kozlov et al., 2017; Şekercioğlu et al., 2016). Moreover, a recent study showed that bird diversity increases human life satisfaction in Europe (e.g., cultural service; Methorst et al., 2021). However, the focus of our study was on agricultural systems and as such, the most essential service upon which smallholder farmers depends, is pest removal by insectivorous birds (García et al., 2020; Maas et al., 2015; Olimpi et al., 2020). The stronger losses of those insectivorous birds is thus particularly worrying in the context of the rapid urban expansion of Bangalore (i.e., built-up area increases of 176% between 1991 and 2018 in our north transect; see Nautiyal et al., 2020), which is swallowing the surrounding agricultural landscapes. Additionally, this rapid urban development, compared to cities in temperate areas, is recent and still in progress. It is therefore likely that the consequences on biodiversity are not fully manifested yet and that an Extinction Debt is still to be paid. There exists, however, ways to promote urban bird communities in urban environments. For instance, it has been demonstrated that urban green areas (e.g., urban parks) can support a high cross taxon biodiversity (Pinho et al., 2016). Additionally, these urban green areas can enhance bird functional diversity (Schütz & Schulze, 2015) while other studies have found that street trees can mitigate the negative effects of urbanization on birds (De Castro Pena et al., 2017). Lin et al. (2015) estimated that the biodiversity and ecosystem services of urban agriculture can have high environmental and societal benefits for cities, potentially exceeding that of urban parks, especially when native plant diversity is increased and impervious area reduced (Lin et al., 2015). There is an urgent need to implement such conservation measures in urban planning to foster the agricultural biodiversity and associated functions and services within cities.

5 | CONCLUSIONS

We demonstrated strong evidence of taxonomic and functional homogenization of farmland bird communities with increasing urbanization that was consistent across all seasons. The amount of grey area (e.g., buildings and sealed surfaces) in the landscape was the best predictor to explain non-linear β -diversity patterns along the urbanization gradient. Both taxonomic and functional β -diversity were driven by species and functional trait loss (i.e., nestedness) with increasing distances in grey area between sites, whereas few functionally similar species (i.e., urban tolerant) became increasingly dominant. Urbanization filtered out species with particular functional traits (i.e., insectivorous birds) and urban communities thus represent an impoverished subset of rural communities.

While biodiversity and associated ecosystem functions are globally declining, urban land cover is projected to increase by 1.2 million km² by 2030 (Seto et al., 2012). Urbanization hence represents a serious threat to ecosystem functioning. As we found evidence of taxonomic and functional homogenization, this decrease of taxonomic and functional diversity could significantly impair the resilience of urban agroecosystems and may in turn affect food production systems by disrupting crucial ecosystem services provided by local farmland bird communities. This concern is especially relevant for countries from the Global South where the actual and future urbanization hotspots are located and where urban agriculture plays an increasingly important role for food security (Bai, 2012; Thebo et al., 2014).

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTIONS

T.T., I.G. and A.W. conceived and designed the study; V.R. collected the bird data; N.N. processed the landscape data; T.T., I.G. and C.W. conceived the analyses; A.W. compiled all data; G.M. conducted the analyses; G.M. wrote the manuscript and all authors revised it.

DATA AVAILABILITY STATEMENT

All data supporting the results of this study along with the R-script are openly available in *Dryad* at <https://doi.org/10.5061/dryad.rn8pk0p9w>.

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SUPPORTING INFORMATION

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