Supplementary information

Land-use change erodes avian functional integrity and ecosystem resilience

Daniel Sol*, Lisieux Fuzessy* & Sandrine Pavoine

*Corresponding authors: d.sol@creaf.uab.cat, lfuzessy@gmail.com

Supplementary Methods

Survey data

The North American Breeding Bird Survey (BBS) is one of the longest-running and most extensive wildlife monitoring programs worldwide, providing essential information on ecosystem health, conservation priorities, and long-term population dynamics[27,31]. The survey follows a standardized roadside design, with more than 4,000 fixed routes distributed across all ecoregions in North America. Each route is sampled once per year during the breeding season (late May to early July, depending on latitude), when birds are most vocally active. Skilled volunteers begin counts at sunrise and record all individuals seen or heard during three-minute point counts at 50 fixed stops along a route, each with a 400-meter radius. For this study, we restricted the dataset to routes within the United States, which offer the longest temporal coverage. Specifically, we analysed data from 2000 to 2023, as this period provides the largest set of available routes, excluding 2020 when no surveys were conducted due to pandemic-related shutdowns. To further ensure methodological consistency, we included only routes with the full 50 stops and those conducted under the most stringent survey protocol (RPID = 101). We finally excluded surveys conducted under adverse weather conditions such as high wind or rain, which can reduce detectability[29]. This resulted in survey data for 5,688 study sites across 83 ecoregions monitored over 23 years.

Defining community assemblages

In our analyses, we defined an avian assemblage as the set of species co-occurring in the same environment at the same time. Identifying such communities critically depend on selecting an appropriate spatial scale. Most previous studies using BBS data have relied on the entire route as the unit of analysis, pooling all point counts across the route. Such a spatial scale, while appropriate for the purpose of these studies, is problematic for community analyses because routes extend over more than 40 km and often encompass multiple habitat types. This may lead to the inclusion of non-coexisting species and to the misattribution of land-use effects to areas that certain species did not actually use. Following Haddou et al.[29], we opted by subdividing every route into five equal segments of 10 stops each. These segments (survey sites, hereafter) provided a closer alignment between bird co-occurrences and the surrounding land cover, and served as our fundamental spatial units of analysis. To ensure better comparability across assemblages, we also limited analyses to terrestrial species. This yielded occurrence data for 510 avian species.

A challenge in identifying species belonging to the same community is imperfect detection: some species may go undetected even when present in the site during surveys. Because detectability varies among species and across space and time, this can result in underestimated occupancy and biased representations of community composition. To tackle this problem, we employed hierarchical occupancy models to explicitly separate the ecological process of occupancy from the observation process of detection[49]. These models allowed us to estimate the likelihood that a species was present at a study site in a given year, even if it was not directly observed (ψ). Non-detection can occur when the detection probability is low, making it plausible that a species is present despite not being recorded. In such cases, the model also considers environmental predictors, which, if indicative of suitable habitat, increase the estimated probability of presence. By explicitly correcting for imperfect detection, hierarchical occupancy models thus avoid the conflation of detection bias with ecological signal.

We used the single-season occupancy model of MacKenzie et al.[49], as implemented in the *R* package *unmarked*[50,51]. For each species in each year, we fitted a model across all survey sites within the geographic range of the species (defined as the ecoregions where the species was detected that year), using the ten point-counts at each site as spatial replicates to account for detectability[52]. Since the occurrence of a species can vary according to environmental conditions, we described habitat variation through a correspondence analysis based on the proportion of pixels from eight land cover categories from the USGS classification system: barren, crop, forest, grass, pasture, urban high, urban low, and wet. The two first correspondence dimensions were included in the occupancy submodel, along with altitude, to capture the effects of habitat on occupancy. Additionally, the detection submodel was refined by including time of day (as birds are less active at midday than in the morning or afternoon) and the proportion of forest cover, because dense vegetation can reduce detectability. Due to frequent convergence issues, we were unable to include observer identity as a factor to account for differences in expertise. Nevertheless, our analyses demonstrate that this omission does not affect the overall conclusions. Convergence issues still persisted in a small fraction of cases (<0.002% of cases), requiring further model simplification by removing non-significant predictors of the detection submodel.

Community diversity metrics

The expected number (N^*) of other species co-occurring with a given species in the assemblage was estimated as:

$$N^* = \frac{\sum_{i=1}^{N} \sum_{j=1, j \neq i}^{N} o_i o_j}{\left(\sum_{k}^{N} o_k \right)} = \sum_{i=1}^{N} \frac{o_i}{\sum_{k}^{N} o_k} \sum_{j=1, j \neq i}^{N} o_j$$

where N is the number of species, and o_i is the probability of occurrence of species i.

Functional diversity (Q^*) was quantified for each assemblage at each survey site and year using a standardized version of Rao's quadratic entropy framework[32–34] based on estimated occupancy probabilities. Mathematically, Q^* is expressed as follows:

$$Q^* = \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} o_i o_j d_{ij}}{\left(\sum_{k}^{N} o_k \right)} = \sum_{i=1}^{N} \frac{o_i}{\sum_{k}^{N} o_k} \sum_{j=1}^{N} o_j d_{ij}$$

where d_{ij} is the functional dissimilarity between species i and j ($0 \leq d_{ij} < \leq 1$, for all i,j). Thus, Q^* can be interpreted as the expected number of functionally distinct species co-occurring in the assemblage with a focal species, where each species is counted according to its degree of functional dissimilarity. Both N^* and Q^* are expressed in units of species numbers minus one, making them ecologically interpretable as expected species counts. From Q^* and N^*, we derived a measure of functional redundancy index as: $R^* = 1 - Q^*$. This index estimates the expected number of functionally similar species to a focal species.

For Q^* and R^*, functional dissimilarity and similarity matrices were computed for each assemblage using Gowers distance metric, based on morphological traits and diet variables. For morphology, we used seven morphological traits from AVONET[53]: beak length (culmen), beak length (tip-to-nares distance), beak depth, beak width, tail length, tarsus length and wing length. Most traits in our dataset covaried strongly with body size, with the exception of the hand–wing index. Following previous studies[23], we accounted for this size dependence using a two-step principal component analysis (PCA) that reduced seven linear morphometric traits into three niche axes representing distinct ecological functions. We first conducted separate PCAs on trophic traits (beak morphology) and locomotory traits using all species. In both cases, the first principal component primarily captured body size variation, so we retained the second component as a size-independent axis of functional variation. Next, we performed a third PCA on the first components of the trophic and locomotory analyses, using the resulting first axis to represent overall body size. For diet, we used BirdBase[54], with diet categories representing the proportional contribution by weight of invertebrates (IN), fruits (FR), nectar (NE), seeds (SE), vertebrates (VE), fish (FI), scavenged items or carrion (SC), plant matter (PL), and miscellaneous food items (MS) to a species' diet. We used a weighted Gower distance that balanced the contribution of morphology and diet by assigning equal weight to each trait group.

Classifying land-use change trajectories

We quantified long-term land-use change for each sampling site using annual proportions of cropland, pasture, and urban land cover. Urban land use was defined as the sum of high- and low-intensity urban cover. For each site and land-use type, time series were first screened for missing values and ordered chronologically. For sites with five or more years of data, we evaluated nonlinear temporal trajectories using generalized additive models (GAMs), as implemented in the R-package 'mgcv'[55]. Specifically, land-use proportion was modelled as a smooth function of year using thin-plate regression splines and restricted maximum likelihood estimation. To avoid overfitting in shorter time series, the basis dimension of the smooth was constrained to a maximum of five knots or one fewer than the number of observations, whichever was smaller. Sites exhibiting negligible temporal variance in land-use proportion were classified as stable without fitting a GAM. For GAM-fitted time series, the direction of land-use change was determined from the mean first derivative of the fitted smooth across the observation period. Positive mean derivatives indicated increasing land use, negative mean derivatives indicated decreasing land use, and derivatives within a small tolerance threshold were classified as no change. When GAM fitting or derivative estimation was not possible due to numerical instability, trend direction was inferred using net change between the first and last observation as a fallback. This approach ensured that nonlinear dynamics were captured when sufficient temporal information was available, while avoiding spurious inference for short or invariant time series. Each site–land-use combination was ultimately assigned to one of three categories—increase, decrease, or no change—providing a consistent and interpretable classification of land-use trajectories across the study region.

Modelling baseline differences across habitats in species richness and functional diversity

To provide a historical baseline, we first examined whether species richness was lower in anthropogenically altered habitats (urban areas, croplands, and pastures) when compared to natural habitats (forests and grassland–shrublands) at the start of the time series (year 2000). Primary site habitats were defined as those covering ≥50% of the site area; only sites that could be assigned to a primary habitat were included in the analysis (N = 4288 assemblages). We modelled each response variable (Q*, N* or R*) as a function of habitat and potential environmental confounds using a general linear mixed-effects (glmm) framework. The fixed effects included the primary habitat (urban, crops, pastures, grass and forest), and three potential confounds: habitat heterogeneity (Shannon diversity index of all land cover proportions), latitude and elevation. We initially tested all quadratic terms and interactions, but retained only those that were statistically significant. The model was fitted using the `lme` function from *nlme* package[56] in R, with route included as a random intercept to account for spatial clustering. Model assumptions, including normality of residuals and homogeneity of variance, were assessed to ensure the validity of the results.

Modelling temporal effects of land use intensification on functional diversity

We investigated changes in biodiversity across 5,688 assemblages over 23 years.
We tested whether land-use intensification explains changes in functional diversity over time using a within–between decomposition approach (also referred to as within-subject centering)[39]. This method separates temporal (within-site) effects of land use from cross-sectional (between-site) effects in longitudinal data. Our primary interest was the within-site effect, defined as the annual deviation of land use from each site's long-term mean. This effect quantifies how temporal variation in land use within a site—whether arising from gradual trends, step changes, or short-term fluctuations—is associated with

changes in functional diversity. The between-site effect was included to control for baseline habitat differences among sites, ensuring that within-site estimates are not confounded by spatial heterogeneity. It was calculated as the average proportion of human-altered habitats across all years for each site, thereby capturing persistent differences among sites (e.g. sites dominated by human-altered habitats consistently exhibiting lower functional diversity). To further control for temporal confounding shared across sites (e.g. climatic variation or sampling effects), year was included as a fixed-effect factor in all models. In addition, we evaluated alternative model specifications allowing for lagged, accumulated, and non-linear relationships between land-use intensification and functional diversity. These extensions were used to account for delayed ecological responses, legacy effects, and extinction debts, whereby changes in biodiversity may occur several years after land-use change, as well as for cumulative impacts arising from prolonged exposure to human-altered habitats. Non-linear relationships were considered to allow for threshold responses and saturation effects, reflecting the possibility that functional diversity responds disproportionately to land-use change once certain levels of habitat alteration are exceeded. These models were run in *nlme* package[39], assuming a Gaussian distribution of errors and accounting for both spatial and temporal dependence. Latitude was included as a fixed effect (along with habitat heterogeneity and altitude) to capture the latitudinal gradient of biodiversity, while sites nested within routes were included as random intercepts to account for repeated measurements and unmeasured site-level heterogeneity. We also examined the effects of longitude and survey site order; however, these fixed effects were not significant and were therefore excluded from the final models. Temporal autocorrelation within sites was modelled explicitly using a first-order autoregressive correlation structure (AR(1)), allowing observations closer in time to be more strongly correlated. This hierarchical spatiotemporal structure accommodated repeated measurements within sites, spatial clustering within routes, and latitudinal variation across sites. Residuals showed no additional detectable spatial or temporal dependence, indicating that this structure was appropriate. All numerical predictors were standardized to zero mean and unit variance to facilitate comparison of effect sizes and improve model convergence.

Assessing temporal stability in functional diversity

To evaluate temporal stability, we summarized functional diversity and predicted species richness in terms of their mean, standard deviation, and coefficient of variation across years, focusing on study sites monitored for at least 15 years and that had suffered minimal land-use change during the 23 years of study (<5% change in urban, cropland, or pasture cover; N = 3974 sites). Stability was expressed as the inverse of the coefficient of variation (1/CV), a widely used measure in studies of the diversity–stability relationship[57]. High values indicate that diversity fluctuated little through time, suggesting high stability. Then, we used general linear mixed-effects to test whether stability can be explained by functional redundancy and proportion of the survey site that was disturbed by urbanisation, crop expansion or pastures (all averaged over the years), including habitat heterogeneity and altitude as fixed effects and route as random effect.

Structural equation modelling (SEM)

We used a SEM to examine the direct and indirect effects of land-use and community properties on functional stability. The analysis was implemented using piecewise structural equation modelling in the R-package piecewiseSEM[58], which allows the inclusion of mixed-effects models to account for nested data structures. Specifically, we fitted linear mixed-effects models for each endogenous variable, including random intercepts for route to account for spatial clustering. The model included all plausible paths based on ecological theory, linking land-use variables (Urban, Crop, Pasture, Heterogeneity) to community properties (functional redundancy, species richness of generalists and habitat heterogeneity) and, ultimately, to functional stability.

49. MacKenzie, D. I. *et al.* Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. *Ecology* **83**, 2248–2255 (2002).

50. Fiske, I. & Chandler, R. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *J. Stat. Soft.* **43**, 1–23 (2011).

51. Kellner, K. F. *et al.* The unmarked R package: Twelve years of advances in occurrence and abundance modelling in ecology. *Methods Ecol. Evol.* **14**, 1408–1415 (2023).

52. Jiménez-Franco, M. V. *et al.* Use of classical bird census transects as spatial replicates for hierarchical modeling of an avian community. *Ecol. Evol.* **9**, 825–835 (2019).

53. Tobias, J. A. AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* (2021).

54. Şekercioğlu, Ç. H. *et al.* BIRDBASE: A Global Dataset of Avian Biogeography, Conservation, Ecology and Life History Traits. *Sci Data* **12**, 1558 (2025).

55. Wood, S. N. Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models. *J. R. Stat. Soc. Ser. B. Stat. Methodol.* **73**, 3–36 (2011).

56. *Mixed-Effects Models in S and S-PLUS*. (Springer-Verlag, New York, 2000). doi:10.1007/b98882.

57. Hooper, D. U., III, F. S. C. & Ewel, J. J. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35 (2005).

58. Lefcheck, J. S. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).

Supplementary tables

Supplementary Table 1: Biodiversity differences across main land cover types.

	Species richness (N*)			**Functional diversity (Q*)**			**Functional redundancy (R*)**		
Predictors	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*
Intercept	36.836	0.443	**<0.001**	4.177	0.051	**<0.001**	33.383	0.400	**<0.001**
Crop-dominated	-2.617	0.311	**<0.001**	-0.299	0.035	**<0.001**	-2.338	0.285	**<0.001**
Pasture-dominated	0.609	0.308	**0.048**	0.077	0.034	**0.023**	0.552	0.282	0.050
Grass-dominated	-2.410	0.317	**<0.001**	-0.268	0.036	**<0.001**	-2.193	0.291	**<0.001**
Forest-dominated	1.806	0.313	**<0.001**	0.147	0.034	**<0.001**	1.687	0.287	**<0.001**
Heterogeneity	0.127	0.301	0.672	0.025	0.033	0.454	0.106	0.276	0.701
Latitude	0.766	0.251	**0.002**	0.068	0.031	**0.027**	0.697	0.224	**0.002**
Altitude	-3.120	0.138	**<0.001**	-0.309	0.016	**<0.001**	-2.861	0.126	**<0.001**
Latitude^2	-0.867	0.194	**<0.001**	-0.009	0.024	0.712	-0.862	0.173	**<0.001**
Altitude^2	0.483	0.045	**<0.001**	0.053	0.005	**<0.001**	0.443	0.041	**<0.001**
Heterogeneity^2	0.152	0.026	**<0.001**	0.009	0.003	**0.006**	0.148	0.023	**<0.001**
Crop-dominated*Heterogeneity	0.917	0.305	**0.003**	0.105	0.034	**0.002**	0.819	0.280	**0.003**
Pasture-dominated*Heterogeneity	-0.232	0.310	0.455	-0.044	0.034	0.194	-0.194	0.284	0.494
Grass-dominated*Heterogeneity	0.758	0.312	**0.015**	0.097	0.035	**0.005**	0.673	0.285	**0.018**
Forest-dominated*Heterogeneity	-0.267	0.307	0.385	-0.033	0.034	0.334	-0.240	0.282	0.395
Random Effects									
σ^2	0.41			0.01			0.33		
τ_{00}	68.20_{route}			1.00_{route}			54.18_{route}		
ICC	0.99			0.99			0.99		
N	1070_{route}			1070_{route}			1070_{route}		
Observations	4288			4288			4288		
Marginal R^2 / Conditional R^2	0.169 / 0.995			0.122 / 0.995			0.178 / 0.995		

Supplementary Table 2: Impact of land use on species richness and functional diversity. Fixed-effect estimates (± SE) from linear mixed-effects models evaluating the effects of land use and environmental covariates on species richness, functional diversity, and functional redundancy. Models included random intercepts for route and survey site and accounted for temporal autocorrelation using an AR(1) structure. All predictors were standardized prior to analysis. Significant effects are shown in bold (p < 0.05).

	Species richness (N*)			**Functional diversity (Q*)**			**Functional redundancy (R*)**		
Predictors	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*
Intercept	35.486	0.258	**<0.001**	4.139	0.028	**<0.001**	32.073	0.233	**<0.001**
Urban (within)	-0.135	0.017	**<0.001**	0.006	0.002	**0.015**	-0.139	0.015	**<0.001**
Crop (within)	0.086	0.023	**<0.001**	0.015	0.003	**<0.001**	0.072	0.020	**<0.001**
Pasture (within)	0.168	0.023	**<0.001**	0.016	0.003	**<0.001**	0.153	0.020	**<0.001**
Urban (among)	-0.016	0.032	0.622	0.002	0.004	0.655	-0.016	0.028	0.575
Crop (among)	-1.134	0.054	**<0.001**	-0.110	0.007	**<0.001**	-1.025	0.047	**<0.001**
Pasture (among)	0.046	0.044	0.288	0.028	0.006	**<0.001**	0.024	0.038	0.540
Latitude	0.745	0.250	**0.003**	0.029	0.027	0.281	0.707	0.225	**0.002**
Altitude	-2.009	0.133	**<0.001**	-0.258	0.016	**<0.001**	-1.761	0.118	**<0.001**
Heterogeneity	0.283	0.037	**<0.001**	0.058	0.005	**<0.001**	0.226	0.033	**<0.001**
Random Effects									
σ^2	12.30			0.27			9.34		
τ_{00}	$8.64_{\text{survey\_site}}$			$0.93_{\text{survey\_site}}$			$7.81_{\text{survey\_site}}$		
	0.00_{route}			0.00_{route}			0.00_{route}		
ICC	0.41			0.77			0.46		
N	$5467_{\text{survey\_site}}$			$5467_{\text{survey\_site}}$			$5467_{\text{survey\_site}}$		
	1124_{route}			1124_{route}			1124_{route}		
Observations	112171			112171			112171		
Marginal R^2 / Conditional R^2	0.185 / 0.521			0.067 / 0.789			0.175 / 0.551		

Supplementary Table 3: Land-use intensification and changes in species richness and functional diversity. The model is restricted to sites that have suffered increased land-use intensification. Fixed-effect estimates (± SE) from linear mixed-effects models evaluating the effects of land use and environmental covariates on species richness, functional diversity, and functional redundancy for sites that have experienced increases in land use intensification. Models included random intercepts for route and survey site and accounted for temporal autocorrelation using an AR(1) structure. All predictors were standardized prior to analysis. Significant effects are shown in bold ($p < 0.05$).

	Species richness (N*)			**Functional diversity (Q*)**			**Functional redundancy (R*)**		
Predictors	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*
(Intercept)	35.521	0.253	**<0.001**	4.142	0.027	**<0.001**	32.106	0.229	**<0.001**
urban within z	-0.152	0.017	**<0.001**	0.004	0.002	0.054	-0.155	0.015	**<0.001**
crop within z	0.077	0.023	**0.001**	0.015	0.003	**<0.001**	0.064	0.021	**0.002**
pasture within z	0.159	0.023	**<0.001**	0.016	0.003	**<0.001**	0.145	0.020	**<0.001**
urban mean z	-0.015	0.033	0.647	0.002	0.004	0.646	-0.015	0.029	0.603
crop mean z	-1.127	0.055	**<0.001**	-0.109	0.007	**<0.001**	-1.019	0.049	**<0.001**
pasture mean z	0.074	0.045	0.101	0.031	0.006	**<0.001**	0.049	0.040	0.218
lat z	0.786	0.245	**0.001**	0.035	0.027	0.196	0.742	0.222	**0.001**
elev z	-2.267	0.145	**<0.001**	-0.289	0.018	**<0.001**	-1.984	0.129	**<0.001**
heter z	0.309	0.039	**<0.001**	0.062	0.005	**<0.001**	0.248	0.034	**<0.001**
Random Effects									
σ^2	12.40			0.28			9.41		
τ_{00}	8.45 $_{\text{survey\_site}}$			0.92 $_{\text{survey\_site}}$			7.64 $_{\text{survey\_site}}$		
	0.00 $_{\text{route}}$			0.00 $_{\text{route}}$			0.00 $_{\text{route}}$		
ICC	0.41			0.77			0.45		
N	5135 $_{\text{survey\_site}}$			5135 $_{\text{survey\_site}}$			5135 $_{\text{survey\_site}}$		
	1120 $_{\text{route}}$			1120 $_{\text{route}}$			1120 $_{\text{route}}$		
Observations	105441			105441			105441		
Marginal R^2 / Conditional R^2	0.215 / 0.533			0.080 / 0.787			0.204 / 0.561		

Supplementary Table 4: Synergic and antagonistic effects of land-use drivers on species richness and functional diversity.

	Species richness (N*)			**Functional diversity (Q*)**			**Functional redundancy (R*)**		
Predictors	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*
Intercept	35.483	0.258	**<0.001**	4.139	0.028	**<0.001**	32.071	0.233	**<0.001**
Urban (within)	-0.134	0.017	**<0.001**	0.006	0.002	**0.014**	-0.138	0.015	**<0.001**
Crop (within)	0.086	0.023	**<0.001**	0.015	0.003	**<0.001**	0.073	0.020	**<0.001**
Pasture (within)	0.169	0.023	**<0.001**	0.016	0.003	**<0.001**	0.154	0.020	**<0.001**
Urban (among)	-0.015	0.032	0.639	0.002	0.004	0.698	-0.015	0.028	0.600
Crop (among)	-1.135	0.054	**<0.001**	-0.111	0.007	**<0.001**	-1.025	0.048	**<0.001**
Pasture (among)	0.044	0.044	0.317	0.027	0.006	**<0.001**	0.021	0.039	0.580
Latitude	0.745	0.250	**0.003**	0.029	0.027	0.278	0.707	0.225	**0.002**
Altitude	-2.010	0.133	**<0.001**	-0.258	0.016	**<0.001**	-1.761	0.118	**<0.001**
Heterogeneity	0.282	0.037	**<0.001**	0.058	0.005	**<0.001**	0.225	0.033	**<0.001**
Urban*Crop (within)	0.005	0.007	0.451	-0.000	0.001	0.900	0.005	0.006	0.378
Urban*Pasture (within)	-0.008	0.009	0.330	-0.002	0.001	0.138	-0.007	0.008	0.387
Crop*Pasture (within)	-0.004	0.004	0.338	-0.001	0.001	0.346	-0.003	0.004	0.354
Urban*Crop*Pasture (within)	0.001	0.004	0.799	-0.001	0.001	0.077	0.002	0.003	0.581
Random Effects									
σ^2	12.30			0.27			9.34		
τ_{00}	8.63 $_{\text{survey\_site}}$			0.93 $_{\text{survey\_site}}$			7.81 $_{\text{survey\_site}}$		
	0.00 $_{\text{route}}$			0.00 $_{\text{route}}$			0.00 $_{\text{route}}$		
ICC	0.41			0.77			0.46		
N	5467 $_{\text{survey\_site}}$			5467 $_{\text{survey\_site}}$			5467 $_{\text{survey\_site}}$		
	1124 $_{\text{route}}$			1124 $_{\text{route}}$			1124 $_{\text{route}}$		
Observations	112171			112171			112171		
Marginal R^2 / Conditional R^2	0.185 / 0.521			0.067 / 0.789			0.175 / 0.551		

Supplementary Table 5: Impact of species extinctions and loss of functional diversity. The models quantify changes in functional diversity attributable solely to local extinctions by excluding colonisations. To do so, we established baseline assemblages as species with occupancy probabilities ≥ 0.7 in 2000, and investigated how their functional diversity changed with land use intensification over time.

	Species richness (N*)			**Functional diversity (Q*)**			**Functional redundancy (R*)**		
Predictors	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*
Intercept	18.793	0.200	**<0.001**	10.109	0.067	**<0.001**	9.464	0.135	**<0.001**
Urban (within)	-0.403	0.009	**<0.001**	-0.102	0.003	**<0.001**	-0.289	0.006	**<0.001**
Crop (within)	0.018	0.012	0.126	0.015	0.004	**<0.001**	0.006	0.009	0.466
Pasture (within)	0.112	0.012	**<0.001**	0.030	0.004	**<0.001**	0.087	0.009	**<0.001**
Urban (among)	0.362	0.056	**<0.001**	0.155	0.020	**<0.001**	0.210	0.038	**<0.001**
Crop (among)	-2.485	0.091	**<0.001**	-0.332	0.032	**<0.001**	-2.133	0.063	**<0.001**
Pasture (among)	0.757	0.075	**<0.001**	0.408	0.026	**<0.001**	0.365	0.052	**<0.001**
Latitude	-0.051	0.197	0.797	-0.155	0.067	**0.020**	0.109	0.133	0.411
Altitude	-5.353	0.169	**<0.001**	-1.835	0.058	**<0.001**	-3.582	0.115	**<0.001**
Heterogeneity	-0.800	0.050	**<0.001**	-0.268	0.017	**<0.001**	-0.529	0.035	**<0.001**
Random Effects									
σ^2	3.21			0.43			1.83		
τ_{00}	$6.62_{\text{survey\_site}}$			$2.23_{\text{survey\_site}}$			$4.47_{\text{survey\_site}}$		
	2.13_{route}			0.76_{route}			1.47_{route}		
ICC	0.73			0.87			0.76		
N	$5467_{\text{survey\_site}}$			$5467_{\text{survey\_site}}$			$5467_{\text{survey\_site}}$		
	1124_{route}			1124_{route}			1124_{route}		
Observations	112150			112150			112150		
Marginal R^2 / Conditional R^2	0.713 / 0.923			0.525 / 0.940			0.633 / 0.913		

Supplementary Table 6: Land-use intensification and changes in species richness and functional diversity in generalist species.

	Species richness (N*)			Functional diversity (Q*)			Functional redundancy (R*)		
Predictors	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*
Intercept	9.386	0.067	**<0.001**	3.885	0.029	**<0.001**	6.243	0.041	**<0.001**
Urban (within)	-0.006	0.005	0.214	0.014	0.002	**<0.001**	-0.020	0.003	**<0.001**
Crop (within)	0.059	0.007	**<0.001**	0.028	0.003	**<0.001**	0.033	0.004	**<0.001**
Pasture (within)	0.046	0.007	**<0.001**	0.014	0.003	**<0.001**	0.033	0.004	**<0.001**
Urban (among)	0.023	0.008	**0.005**	0.011	0.004	**0.008**	0.016	0.005	**0.001**
Crop (among)	0.114	0.014	**<0.001**	0.090	0.007	**<0.001**	0.039	0.008	**<0.001**
Pasture (among)	0.079	0.011	**<0.001**	0.045	0.006	**<0.001**	0.041	0.006	**<0.001**
Latitude	0.522	0.065	**<0.001**	0.152	0.028	**<0.001**	0.356	0.040	**<0.001**
Altitude	-0.397	0.035	**<0.001**	-0.200	0.017	**<0.001**	-0.225	0.020	**<0.001**
Heterogeneity	0.056	0.010	**<0.001**	0.041	0.005	**<0.001**	0.013	0.005	**0.015**
Random Effects									
σ^2	1.33			0.35			0.41		
τ_{00}	2.25 $_{\text{survey\_site}}$			0.96 $_{\text{survey\_site}}$			1.39 $_{\text{survey\_site}}$		
	0.00 $_{\text{route}}$			0.00 $_{\text{route}}$			0.00 $_{\text{route}}$		
ICC	0.63			0.73			0.77		
N	5467 $_{\text{survey\_site}}$			5467 $_{\text{survey\_site}}$			5467 $_{\text{survey\_site}}$		
	1124 $_{\text{route}}$			1124 $_{\text{route}}$			1124 $_{\text{route}}$		
Observations	112171			112171			112171		
Marginal R^2 / Conditional R^2	0.118 / 0.673			0.065 / 0.752			0.090 / 0.794		

Supplementary Table 7: Land-use intensification and changes in species richness and functional diversity in invertivorous species.

	Species richness (N*)			Functional diversity (Q*)			Functional redundancy (R*)		
Predictors	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*
Intercept	17.328	0.178	**<0.001**	5.783	0.051	**<0.001**	12.247	0.129	**<0.001**
Urban (within)	-0.123	0.010	**<0.001**	-0.024	0.003	**<0.001**	-0.098	0.007	**<0.001**
Crop (within)	-0.012	0.014	0.369	-0.002	0.005	0.660	-0.010	0.009	0.304
Pasture (within)	0.083	0.014	**<0.001**	0.021	0.005	**<0.001**	0.065	0.009	**<0.001**
Urban (among)	-0.082	0.019	**<0.001**	-0.027	0.006	**<0.001**	-0.055	0.013	**<0.001**
Crop (among)	-1.257	0.032	**<0.001**	-0.400	0.011	**<0.001**	-0.880	0.022	**<0.001**
Pasture (among)	-0.190	0.026	**<0.001**	-0.041	0.009	**<0.001**	-0.147	0.018	**<0.001**
Latitude	-0.059	0.171	0.732	-0.140	0.049	**0.004**	0.074	0.123	0.547
Altitude	-1.068	0.081	**<0.001**	-0.427	0.026	**<0.001**	-0.680	0.056	**<0.001**
Heterogeneity	0.102	0.022	**<0.001**	0.039	0.007	**<0.001**	0.065	0.015	**<0.001**
Random Effects									
σ^2	4.58			0.62			2.15		
τ_{00}	$5.96_{\text{survey\_site}}$			$1.70_{\text{survey\_site}}$			$4.31_{\text{survey\_site}}$		
	0.00_{route}			0.00_{route}			0.00_{route}		
ICC	0.57			0.73			0.67		
N	$5467_{\text{survey\_site}}$			$5467_{\text{survey\_site}}$			$5467_{\text{survey\_site}}$		
	1124_{route}			1124_{route}			1124_{route}		
Observations	112166			112166			112166		
Marginal R^2 / Conditional R^2	0.151 / 0.631			0.112 / 0.763			0.111 / 0.705		

Supplementary Table 8. Land-use intensification and changes in species richness and functional diversity in granivorous species.

	Species richness (N*)			**Functional diversity (Q*)**			**Functional redundancy (R*)**		
Predictors	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*	*Estimates*	*std. Error*	*p*
Intercept	3.949	0.036	**<0.001**	2.187	0.019	**<0.001**	2.509	0.018	**<0.001**
Urban (within)	-0.041	0.002	**<0.001**	-0.008	0.001	**<0.001**	-0.031	0.001	**<0.001**
Crop (within)	0.024	0.003	**<0.001**	0.015	0.002	**<0.001**	0.013	0.002	**<0.001**
Pasture (within)	0.028	0.003	**<0.001**	0.013	0.002	**<0.001**	0.018	0.002	**<0.001**
Urban (among)	0.040	0.004	**<0.001**	0.025	0.002	**<0.001**	0.023	0.002	**<0.001**
Crop (among)	0.164	0.007	**<0.001**	0.117	0.004	**<0.001**	0.090	0.004	**<0.001**
Pasture (among)	0.114	0.006	**<0.001**	0.068	0.003	**<0.001**	0.066	0.003	**<0.001**
Latitude	0.314	0.035	**<0.001**	0.168	0.018	**<0.001**	0.138	0.018	**<0.001**
Altitude	-0.169	0.018	**<0.001**	-0.107	0.010	**<0.001**	-0.079	0.009	**<0.001**
Heterogeneity	0.029	0.005	**<0.001**	0.023	0.003	**<0.001**	0.007	0.003	**0.004**
Random Effects									
σ^2	0.39			0.12			0.09		
τ_{00}	$1.22_{\text{survey\_site}}$			$0.63_{\text{survey\_site}}$			$0.61_{\text{survey\_site}}$		
	0.00_{route}			0.00_{route}			0.00_{route}		
ICC	0.76			0.84			0.87		
N	$5467_{\text{survey\_site}}$			$5467_{\text{survey\_site}}$			$5467_{\text{survey\_site}}$		
	1124_{route}			1124_{route}			1124_{route}		
Observations	112127			112127			112127		
Marginal R^2 / Conditional R^2	0.105 / 0.782			0.082 / 0.851			0.058 / 0.877		

Supplementary Table 9: Impact of land-use drivers on habitat heterogeneity.

	Heterogeneity		
Predictors	*Estimates*	*std. Error*	*p*
(Intercept)	0.007	0.020	0.721
urban within z	0.012	0.001	**<0.001**
crop within z	0.006	0.001	**<0.001**
pasture within z	-0.007	0.001	**<0.001**
urban mean z	0.286	0.011	**<0.001**
crop mean z	-0.155	0.017	**<0.001**
pasture mean z	0.255	0.014	**<0.001**
lat z	0.124	0.020	**<0.001**
elev z	-0.286	0.021	**<0.001**
Random Effects			
σ^2	0.25		
$\tau_{00\ survey\_site}$	0.64		
$\tau_{00\ route}$	0.00		
ICC	0.72		
N_{survey_site}	5467		
N_{route}	1124		
Observations	112171		
Marginal R^2 / Conditional R^2	0.281 / 0.799		

Supplementary Table 10: Direct and indirect effects of the structural equation model of land-use changes (urban, crop, and pasture) on functional diversity stability.

Land use	Direct	Indirect via generalist species richness	Indirect via Functional redundancy	Indirect via hetereogeneity	Total Indirect	Total Effect
Urban	-0.005	0.002	0.002	-0.013	-0.009	-0.014
Crop	0.101	0.009	-0.019	0.003	-0.007	0.094
Pasture	0.019	0.003	0.001	-0.015	-0.011	0.007