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Land-use change erodes avian functional integrity and ecosystem resilience

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Human land-use change is the primary force reshaping ecosystems, selectively excluding disturbance-sensitive taxa and concentrating biodiversity in human-dominated landscapes. Yet the consequences of such reconfigurations for ecosystem functioning and resilience remain uncertain. Theoretical predictions are equivocal because land-use change can both reduce functional redundancy, destabilising ecosystems, and promote disturbance-tolerant species, which may increase stability. Empirically resolving this ambiguity has proven challenging because most large-scale studies rely on static snapshots rather than time-series data, hindering our ability to directly link land-use change to alterations in functional integrity and resilience. Here, we present a continental-scale, temporally resolved analysis of how land-use intensification affects the functional integrity and stability of North American avian communities. We analysed 5,467 assemblages over 22 years, combining occupancy-modelled survey data, comprehensive morphological and dietary trait information for all species, and high-resolution annual land-cover maps of natural and human-modified habitats. We show that urbanisation—the

most extreme form of land-use change—undermine community integrity and in doing so, weakens functional stability. This instability stems from erosion of functional redundancy and is amplified by increased habitat heterogeneity, despite the rise of disturbance-tolerant species. In crop-dominated landscapes, however, stability is maintained despite extreme loss of redundancy, due to the offsetting effects of habitat homogenization and gains in disturbance-tolerant species as well as direct stabilising mechanisms. Thus, land-use change can lead to communities deprived of key ecosystem functions and more exposed to future disturbances, but low redundancy alone does not necessarily imply greater vulnerability.

Anthropogenic land-use change is currently the dominant global driver of biodiversity loss, reshaping ecosystems through agricultural expansion and urbanisation[1,2]. These transformations restructure species assemblages in non-random ways—typically filtering out disturbance-sensitive taxa while favouring those taxa that can tolerate modified habitats[3–8]. Such reassembly can have potentially profound consequences for ecosystem functioning and resilience[2], yet these consequences remain poorly understood[9]. As the conversion of natural habitats to anthropogenic land uses is projected to continue throughout the twenty-first century and beyond, particularly through urbanisation[10,11]—reducing species richness and concentrating what remains into human-dominated landscapes—concerns are growing that the erosion of functional integrity will leave communities not only lacking critical ecosystem functions but also more vulnerable to future disturbances.

Understanding the functional consequences of land-use change remain challenging at landscape scales —where conservation is most relevant[12,13]— because species loss does not translate directly into functional diversity loss, which ultimately underpins ecosystem functioning and resilience[13–15]. Theoretical and experimental evidence shows that when multiple species perform similar ecological roles, the loss of any single species may have little immediate effect on ecosystem functioning, as compensatory responses among functionally redundant species create an insurance effect[16,17]. A major concern

is thus that land-use conversion and intensification can erode functional redundancy, potentially undermining long-term ecosystem functioning[18–20]. Yet even in functionally redundant communities, non-random extinctions that preferentially remove species with particular traits can cause rapid functional diversity loss, thereby altering ecosystem functioning[12,21]. Conversely, communities with low functional redundancy are not inherently vulnerable if anthropogenic land-use change leads to species assemblages that are more resilient to future disturbances—because sensitive species have already been lost and tolerant species dominate[14]. Thus, projecting the enduring impacts of land-use change on ecosystem processes requires understanding both how functional integrity is altered by land-use intensification and how such alteration modifies the resilience of the resulting communities.

Recent empirical research has advanced our understanding of how land-use change affects functional diversity in natural communities, linking intensification to non-random loss of species according to their disturbance-sensitivity and revealing a consistent decline in functional redundancy[9,18,20–23]. However, current evidence remains largely indirect, relying on space-for-time substitution approaches that compare assemblages across habitats[24]. Such a static perspective provides only snapshots of community structure, and does not allow to directly assess how temporal changes in land use drive non-random shifts in species composition and reshape functional diversity. The lack of a temporal perspective also prevents the direct estimation of the impact of land-use change on functional stability[25], forcing researchers to rely on species-extinction simulations based on either random loss scenarios or uncertain rankings of species' sensitivities[23]. Therefore, there is an urgent need to move beyond snapshot comparisons of habitats to assess how temporal changes in land use drive non-random shifts in species composition and reshape functional diversity and ecosystem resilience[26].

Here, we provide a continental-scale, temporally resolved assessment of how land-use intensification affects the functional integrity and stability of terrestrial bird assemblages. Our analyses draw on the North American Breeding Bird Survey (BBS[27]), one of the longest-running and most

comprehensive wildlife monitoring programs worldwide[28,29]. North American birds are one of the best documented case of biodiversity loss, with a third of species and nearly 3 billion individuals lost in the past 50 years[27,28,30,31]. We analysed data from more than 5,400 avian assemblages monitored through standardised surveys from 2000-2023, encompassing 510 terrestrial species across 83 North American ecoregions. Using a quadratic entropy framework[32–34], we estimated species richness, functional diversity, and functional redundancy for each assemblage in each year based on species occupancy probabilities derived from hierarchical occupancy models that account for imperfect detection[35]. Functional diversity and redundancy were calculated from species' morphological and dietary traits, drawing on recently available comprehensive trait data for all species in the assemblages[36]. By matching such comprehensive data with high-resolution, annual land-cover estimates of both natural and human-modified habitats in the sampled sites[37], we moved beyond static snapshots of biodiversity patterns to explore their dynamics over time and space.

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). In line with previous studies[1,6,38], species richness declined along the gradient of increasing human disturbance: it was highest in forest-dominated landscapes, intermediate in pastures, lower in urban areas, and lowest in croplands (**Fig. 1** and **Supplementary Table 1**). The lower species richness in sites dominated by anthropogenic land-uses was associated with lower functional diversity and redundancy (**Fig. 1**), again supporting previous studies[6]. All these patterns remained robust after accounting for other major drivers of species richness, including habitat heterogeneity, elevation, and latitude (**Fig. 1**). Although grassland–shrubland habitats constituted an exception to the general disturbance gradient, this probably reflects that open habitats exclude forest-dependent species and therefore host a more restricted species pool. Biodiversity in croplands and grasslands was notably lower than in other land-cover types but tended to increase with greater landscape heterogeneity (**Fig. 1**).

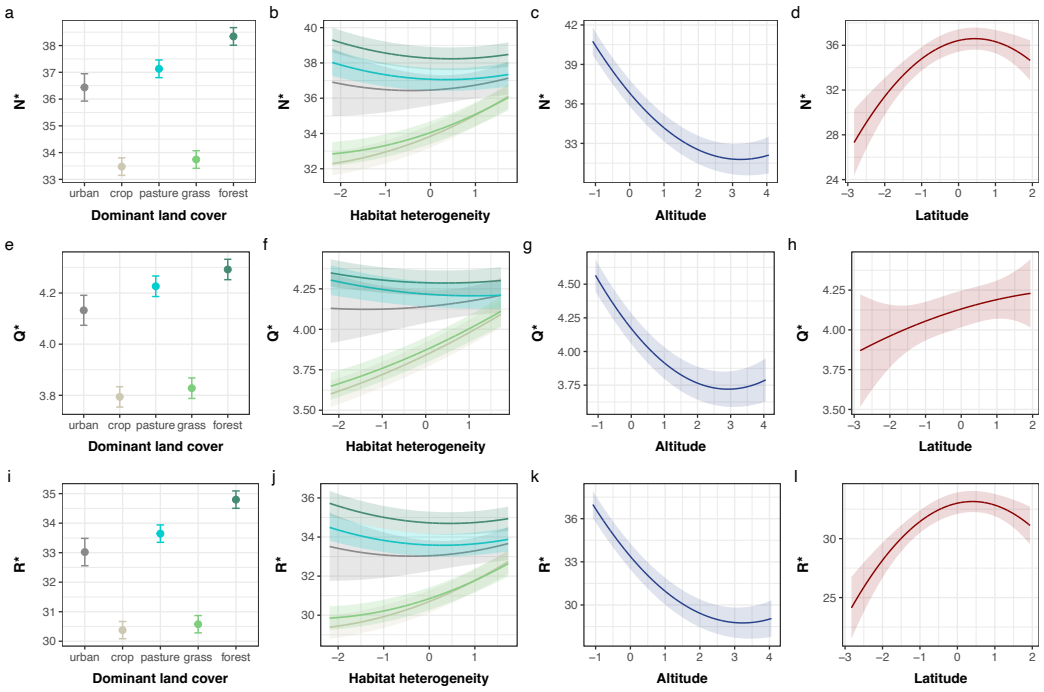


Figure 1 | Habitat differences in biodiversity for the historical baseline, using a space-for-time substitution approach. Plots represent the predicted effects from the models. The figure also shows interactions with habitat heterogeneity and the effects of altitude and latitude. Primary site habitats 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).

While our results suggest that land-use reduces avian diversity, confirming this requires testing whether biodiversity declines track increases in land-use. In North America, agricultural expansion peaked in the 19th–early 20th centuries and later stabilized or declined, while urban expansion accelerated after 2000[38]. To separate historical and contemporary effects, we used a within–between decomposition mixed-effects model[39], partitioning long-term regional effects (between-site) from year-to-year deviations within sites (within-site). As expected, our analyses revealed that land-use change drivers influence biodiversity in contrasting ways through time (**Fig. 2**, **Extended Data Fig. 1** and **Supplementary Table 2**). Temporal increases in urban cover within sites were associated with declines in species richness and functional redundancy, while between-site effects were not significant. Although functional diversity initially increased with urbanisation, this effect was transient and disappeared after a few years. In contrast, cropland and pastures showed strong legacy

effects. Landscapes long dominated by cropland exhibited long-term lower species richness, functional diversity, and functional redundancy (between-site effects), whereas short-term within-site increases produced only small and transient positive responses. Pasture expansion showed similar transient short-term gains combined with longer-term differences, although historical effects were significant only for functional diversity, which increased with pasture cover. Together, these results suggest that the most severe biodiversity changes linked to cropland and pasture occurred in the past, whereas urbanisation is now driving most of the observed contemporary biodiversity change.

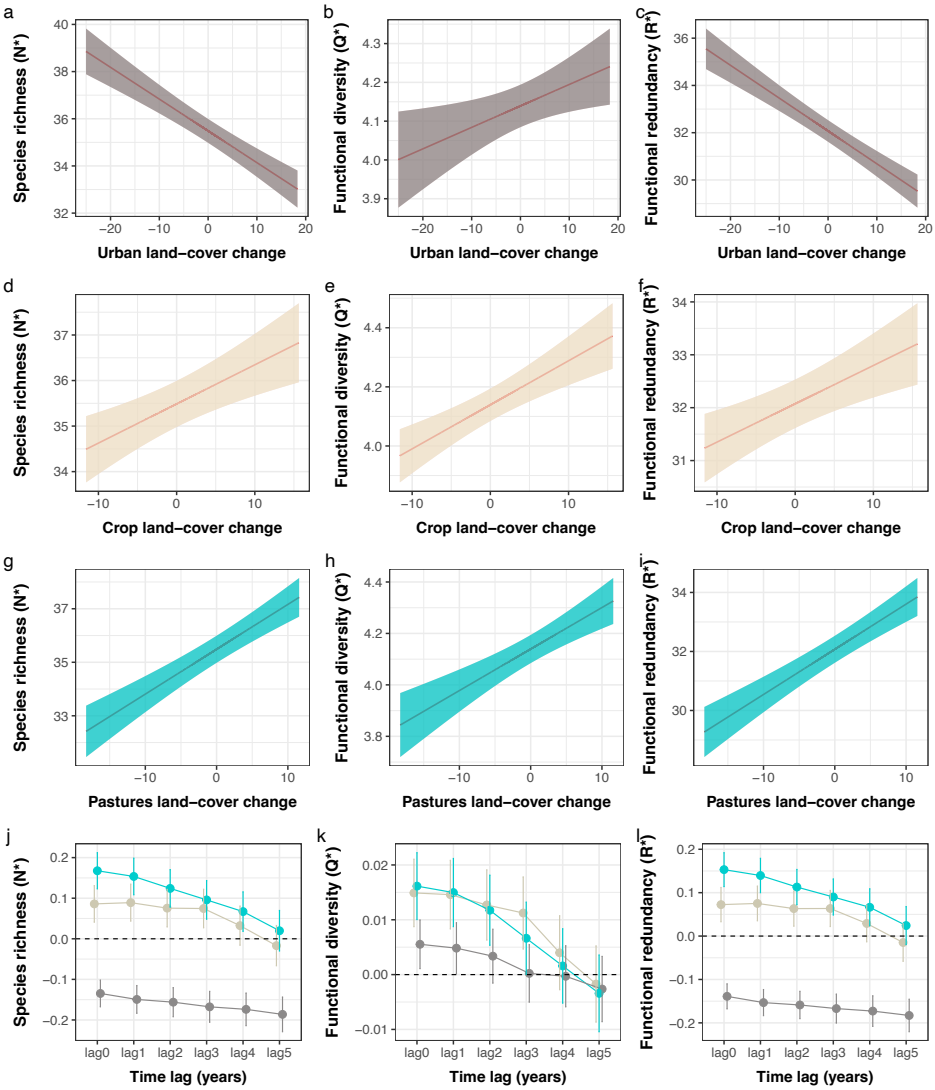


Figure 2 | Effect of land use intensification on temporal changes in species richness, functional diversity, and functional redundancy. Plots represent the predicted within-site effects estimated by the models. **a-i**, changes in biodiversity metrics with temporal changes in land-use cover. For details on the model, see Supplementary Information. **j-i**, lagged responses

of biodiversity metrics to land-use intensification. Lags are in years, so log0 means that the response is measured the same year, lag1 one year later, lag2 two years later and so on. All models account for spatial and temporal autocorrelation, and potential confounding effects of altitude, latitude and habitat heterogeneity.

Although land-use conversion and intensification have globally increased across North America—largely driven by urban expansion—long-term trends remain spatially heterogeneous[38], with cropland and pastures declining in some regions despite remaining dominant land covers (**Extended Data Fig. 2**). Our within–between mixed-effects models accommodate both increases and decreases in land use, but implicitly treat them as opposite sides of the same process. As recovery trajectories may differ from degradation pathways, we tested whether results held when analyses were restricted to sites experiencing increasing land-use intensification. The results were in agreement with our previous results (**Supplementary Table S3**), reinforcing the conclusion that ecosystem alteration is the dominant driver of the observed changes in biodiversity.

Land uses are not randomly distributed: economic growth, population pressure, and infrastructure can simultaneously drive urban, crop, and pasture expansion, potentially producing synergistic or antagonistic effects on biodiversity. We therefore tested interactions among increases in urban, crop, and pasture cover. We found no significant pairwise or three-way interactions for species richness or functional redundancy, and only a small three-way effect for functional diversity, indicating a dampened response when all land uses increased together (**Supplementary Table S4**). Overall, biodiversity responses to these land-use drivers were largely independent, despite their frequent co-occurrence across sites (**Extended Data Fig. 2**).

Land-use change can alter the functional integrity of ecosystems without necessarily reducing functional diversity. This happens when lost species are replaced by others that differ in their ecological roles. To assess whether our previous analyses may have masked such functional degradation, we quantified changes in functional diversity attributable solely to local extinctions by

excluding colonisations occurring after 2000. This approach strengthened the long-term patterns previously observed for crops and pastures, showing that functional diversity declined with increasing cropland area and increased with greater pasture cover (**Supplementary Table S5**). However, unlike our earlier results, the within-site effect of urban cover on functional diversity became negative ($\beta = -0.102$, $p < 0.001$; **Supplementary Table S5**). According to our model, a 5% increase in urbanisation corresponded to declines of approximately 11% in species richness, 5% in functional diversity, and 15% in functional redundancy, relative to the site's mean urban cover. Overall, these findings suggest that ongoing urban expansion and historical agricultural expansion eroded original functional diversity, whereas pastures generally enhanced biodiversity.

The loss of functional integrity caused by local extinctions was not offset by new colonisations, as some functions were largely lost. In particular, invertivores—key regulators of invertebrate populations—were consistently disadvantaged in all land-use changes (**Supplementary Tables S6–S8**), showing marked declines in species richness, functional diversity and functional redundancy at their most relevant temporal scale (within-sites for urban expansion, and among sites for crops and pastures). Instead, generalist and granivorous species generally responded positively to agricultural land uses, particularly cropland, with increases in species richness, functional diversity and functional redundancy over time within and across sites (**Supplementary Tables S6-S8**). Contemporary increases in urban cover (within-site effects) tended to restructure communities by maintaining generalist species richness and increasing their functional diversity, while reducing functional redundancy (**Fig. 3** and **Supplementary Tables S6–S8**). In contrast, granivorous guilds experienced declines in species richness, functional diversity, and functional redundancy as urbanisation increased, mirroring the patterns observed for invertivores. Together, these results point to a pervasive functional simplification of communities under land-use change, with gains in diversity and redundancy largely confined to disturbance-tolerant guilds.

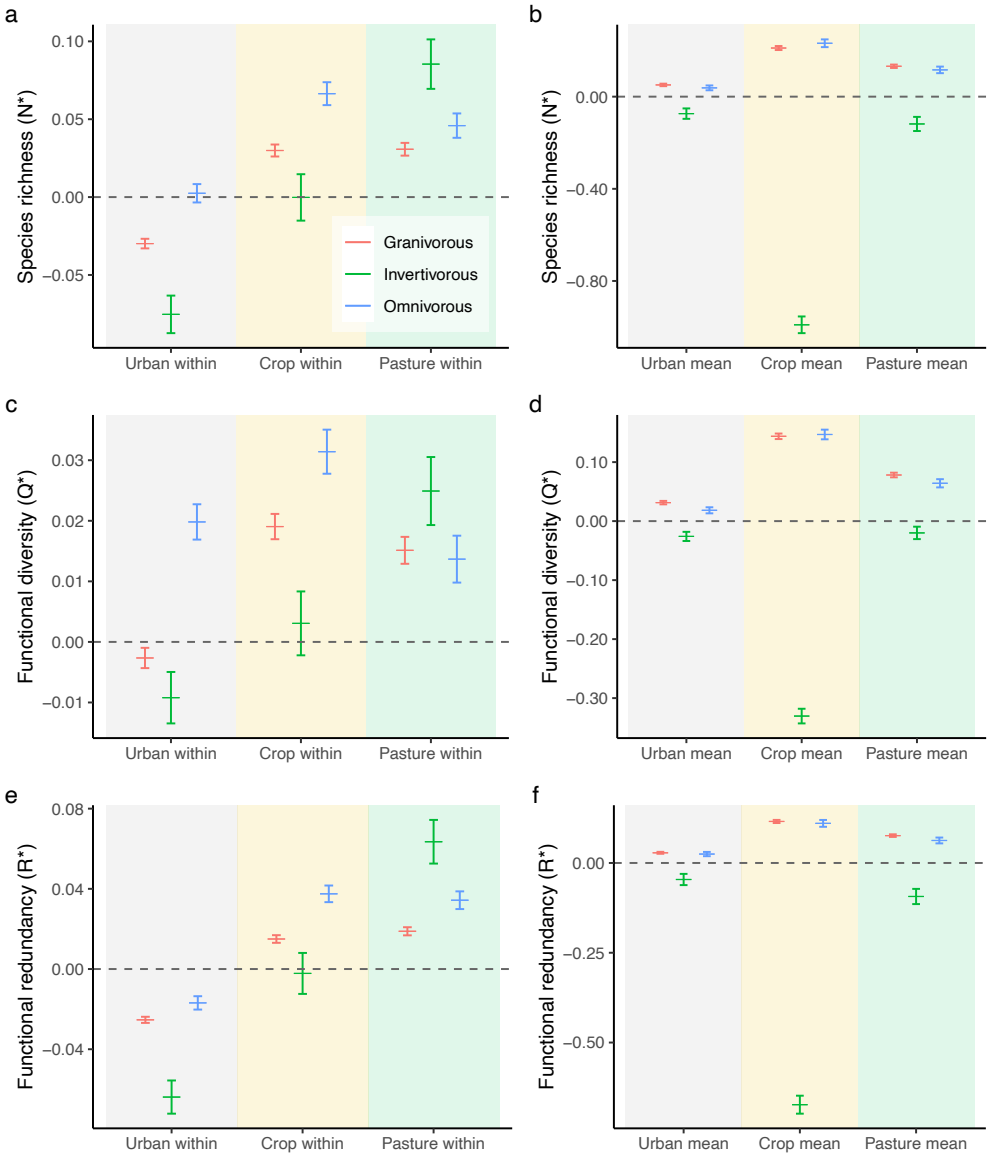


Figure 3 | Effects of land-use intensification on biodiversity metrics within trophic niches. Temporal (within-site) and spatial (mean) effect sizes derived from the models are shown for species richness (S), functional diversity (Q*), and functional redundancy (R*), separated by trophic guilds. Coloured background bands indicate dominant land-use types: urban (grey), crop (yellow), and pasture (green). Error bars represent ±1 standard error. Granivorous (red), invertivorous (green) and generalists (blue).

Declines in functional redundancy should undermine ecosystem stability by reducing the functional insurance that buffers communities against environmental perturbations. However, these potential destabilising effects may be outweighed by a shift toward communities dominated by habitat generalists—as generalism is the main predictor of urban tolerance[6,40]. Land-

use change can also induce changes in local environmental heterogeneity (**Supplementary Table S9)**, which are often assumed to enhance stability through niche complementarity and spatial insurance[41–43] but can also reduce stability by increasing local species turnover[44,45]. To test the relevance of these mechanisms empirically, we quantified the temporal stability of functional diversity as the ratio of its temporal mean to standard deviation[46] at sites monitored for ≥15 years with minimal land-use change (<5% change in urban, cropland, or pasture cover). Functional stability increased with generalist richness and redundancy but declined with habitat heterogeneity (**Fig. 4**). As the influence of these drivers differed among land-use types (**Fig. 4d-f**), we expected functional stability to vary accordingly.

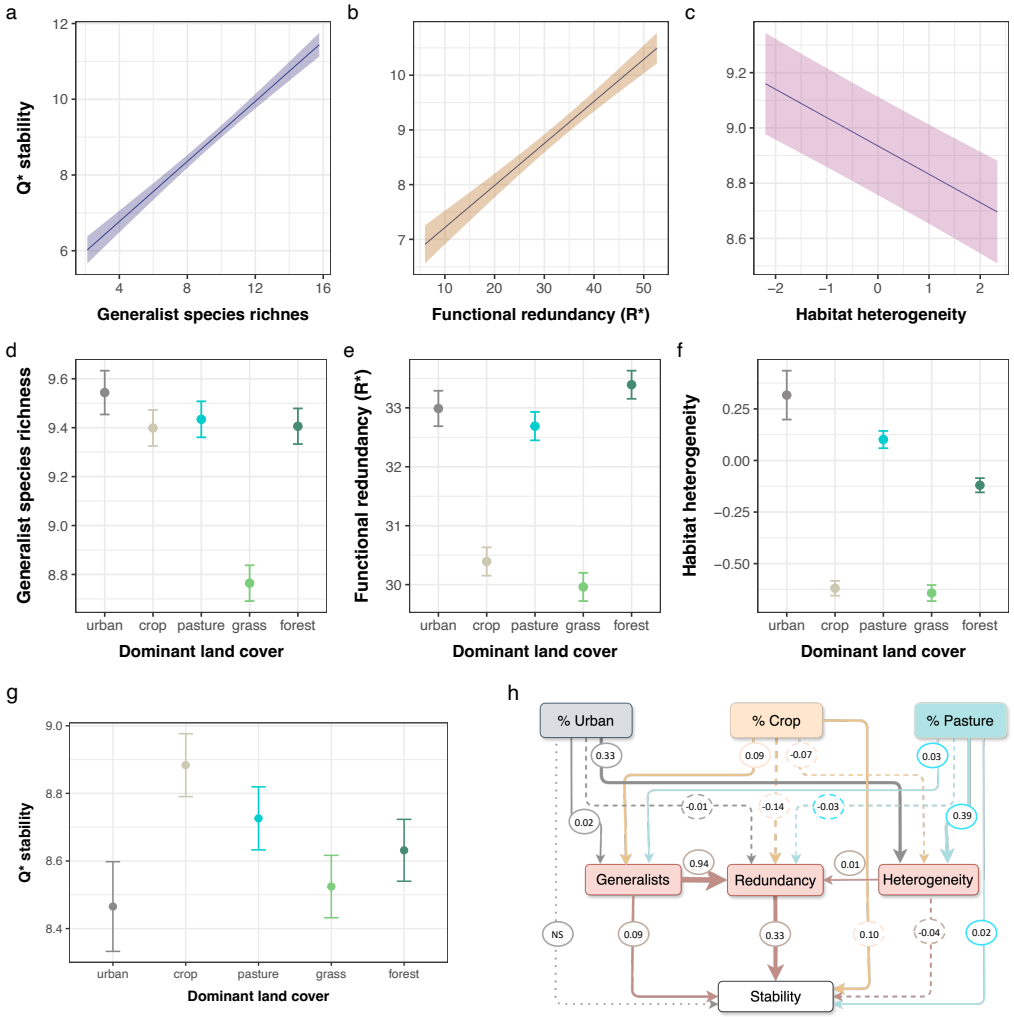


Figure 4 | Functional diversity stability across land cover types. Plots represent the effects predictions of the models. **a-c,** Effects of generalist species richness (a), redundancy (b) and habitat heterogeneity (c) on functional diversity stability (Q* stability). **d-f**, differences across

land cover types in generalist species richness (d), redundancy (e) and habitat heterogeneity (f). **g**, differences across land cover types in functional diversity stability. **h**, path analysis testing causal links (values are standardized path coefficients; NS means non-significant). Analyses are based on the subset of study sites exposed to reduced land use-changes (N = 3974).

We indeed found consistent differences in functional diversity stability across anthropogenic-altered landscapes: stability was lowest in urbanised sites, intermediate in pastures (and similar to those observed in sites dominated by natural habitats), and highest in croplands (**Fig. 4g**). Under our definition, stability can increase through higher mean functional diversity, lower temporal variability, or both[45]. Importantly, drivers that increase variability may still enhance stability if they produce a proportionally larger increase in mean productivity[45]. The lower functional stability observed in urban areas compared to other land covers was primarily driven by temporal variability, which undermines the stabilising influence of increased functional diversity (**Extended Data Fig. 4**). In contrast, croplands and pastures experienced smaller year-to-year fluctuations, enhancing their functional stability.

A structural equation model (SEM) showed that functional diversity stability arises from a combination of direct and indirect effects mediated through functional redundancy, community composition, and habitat heterogeneity (**Fig. 4h** and **Supplementary Table 10**). As expected, loss of functional redundancy emerges as the strongest direct predictor of instability ($\beta = 0.33$, $p < 0.001$), while generalist species richness has a smaller but significant positive direct effect on stability ($\beta = 0.10$, $p = 0.019$) and also indirectly promote it by influencing redundancy ($\beta = 0.94$, $p < 0.001$). Landscape heterogeneity weakly helps stabilise functional diversity by increasing redundancy but its main contribution is generating instability ($\beta = -0.04$, $p < 0.001$). Importantly, according to the SEM these factors are differently affected by land-use drivers, explaining the observed differences in functional stability (**Fig. 4g**). Thus, urbanisation reduces stability primarily by increasing heterogeneity and reducing redundancy—effects that cannot be offset by the presence of generalist species. In contrast, cropland increases overall stability, mainly through a positive direct effect, which is reinforced by indirect pathways via generalist species richness and reduced heterogeneity, outweighing the

negative influence of decreased redundancy. Pasture lands show little net effect on stability, as positive and negative pathways largely balance each other. The direct positive effects of croplands and pastures on stability remain unclear and deserve future research. They may reflect steadier energy inputs, increased spatial asynchrony that stabilizes ecosystem dynamics via a portfolio effect, or the long-standing presence of such land uses, which could have allowed species more time to adapt. Despite uncertainties, our results challenge the view that reduced functional redundancy alone implies greater ecosystem vulnerability. The results instead align with theoretical and experimental work emphasizing the multifaceted nature of ecosystem resilience[14,43,44,47], suggesting that land-use changes can result in communities that differ greatly in their susceptibility to future disturbances despite sharing properties expected to confer stability.

Currently, more resources are invested in biodiversity conservation than ever before. Yet, most global indicators show that threats continue to intensify, more species are becoming at risk, and the provision of ecosystem services is declining[48]. This scenario poses major challenges for biodiversity conservation, underscoring the need to move beyond reactive conservation toward strategies that anticipate and prevent new emerging pressures. Central to this shift is a focus on resilience—ensuring that ecosystems retain their functions and continue delivering essential services. Our analyses contribute to this goal by showing how land-use change erodes avian community integrity and ecosystem functioning, and in doing so, alters ecological stability of natural communities. While these analyses represent a significant step forward by explicitly modelling temporal changes, many uncertainties remain about the underlying mechanisms. To provide a more complete picture, future research will have to consider additional mechanisms, such as spatial and species-abundance asynchronies, as well as refine our understanding of trait–function links, include the impact of climate change and increase the scope to include other ecosystem components besides birds. These improvements will strengthen predictions on the enduring impacts of land-use change on functional integrity and stability of natural communities, and support more effective strategies for managing ecosystems in a rapidly changing world.

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Author contributions

Original idea: D.S. and S.P. Conceptualisation: D.S., L.F and S.P. Methodology: D.S., L.F and S.P. Data collection: L.F. Analysis: D.S and L.F. Funding acquisition: D.S. Writing – original draft: D.S. Writing – review & editing: L.F. and S.P.

Competing interests

Authors declare that they have no competing interests.

Supplementary information

The online version contains supplementary Methods and Tables. The data files and code will be available at Zenodo.

Materials & Correspondence

Correspondence and requests for materials should be addressed to Daniel Sol and Lisieux Fussezy.

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Methods

Survey data

The North American Breeding Bird Survey (BBS) is a long-term, standardized monitoring program based on annual roadside surveys conducted during the breeding season[27,31]. Each route consists of 50 fixed stops where trained observers record all birds seen or heard. We restricted the dataset to U.S. routes surveyed between 2000 and 2023 (excluding 2020), including only routes with the full 50 stops, conducted under the strictest protocol (RPID = 101), and excluding surveys performed under adverse weather conditions[29].

Defining community assemblages

We defined an avian assemblage as the set of species co-occurring at the same place and time. Rather than using entire BBS routes, we subdivided each route into five segments of 10 stops (sites) to better match species co-occurrence and local land cover[29]. The final dataset comprised 5,688 sites across 83 ecoregions monitored over 23 years. We restricted analyses to terrestrial species, resulting in occurrence data for 510 species. To account for imperfect detection and avoid biased estimates of community composition, we used hierarchical single-season occupancy models[49], as implemented in the R package unmarked[50,51]. These models explicitly separate true occupancy from detection probability, allowing us to estimate likelihood that a species was present at a study site in a given year even if it was not directly observed.

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. We computed functional dissimilarity for each assemblage using Gower's distance based on morphology and diet. Morphological data (seven AVONET traits[53]) were reduced into three niche axes using a two-step PCA to separate body size from size-independent functional variation[23]. Diet data (BirdBase[54]) included proportional contributions of major food categories. We applied a weighted Gower distance, giving equal weight to morphology and diet. 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.

Classifying land-use change trajectories

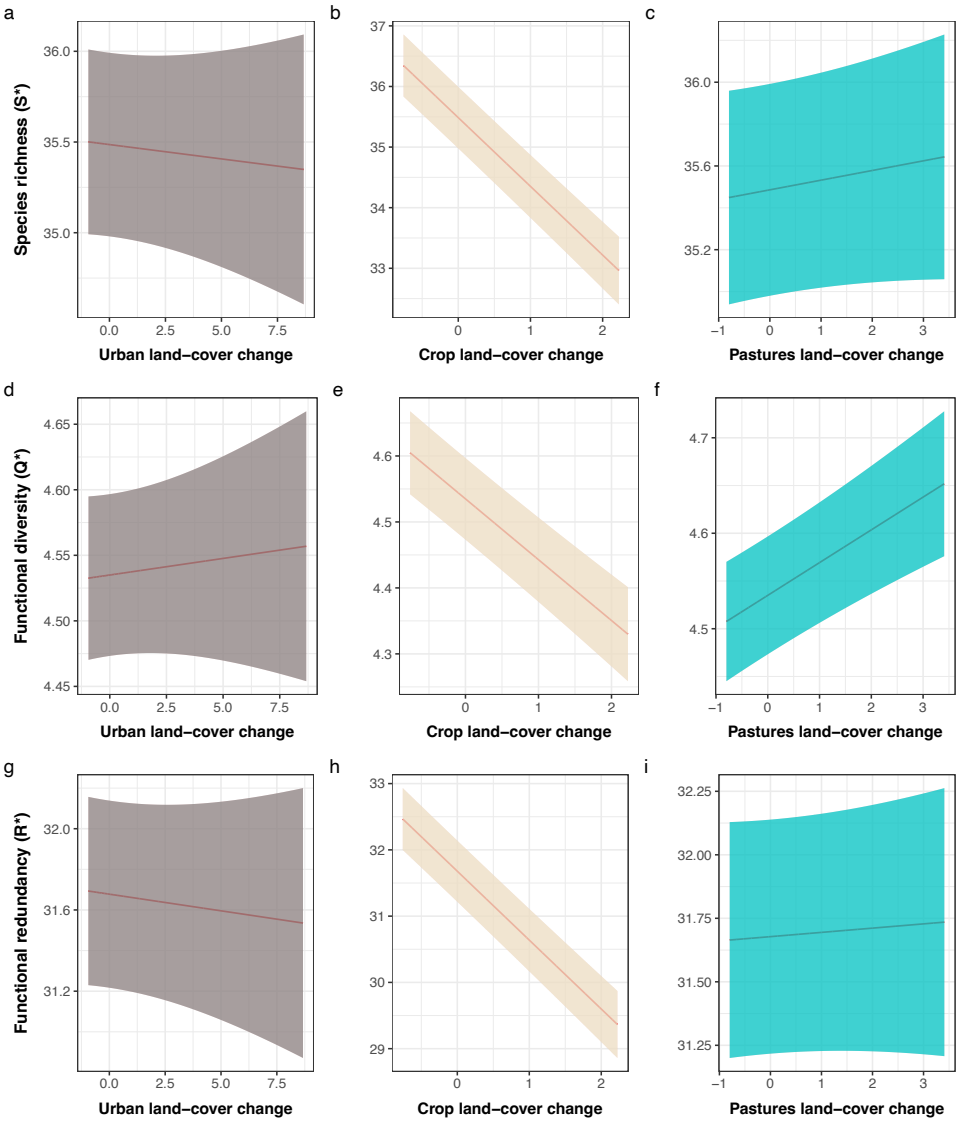
We quantified long-term land-use change at each site using annual proportions of cropland, pasture, and urban cover (high- and low-intensity combined). For sites with five or more years of data, we used generalized additive models (GAMs) in the R-package 'mgcv'[55] to capture potential nonlinear trends, classifying change based on the overall direction of the fitted trajectory. Each site–land-use combination was ultimately assigned to one of three categories—

562 increase, decrease, or no change—providing a consistent and interpretable
563 classification of land-use trajectories across the study region.
564
565 ***Modelling approaches***
566 We analysed biodiversity by means of general linear mixed-effects models, as
567 implemented in the **nlme** package[56] in R. To establish a historical baseline, we
568 tested whether richness and functional diversity were lower in
569 anthropogenically altered habitats (urban areas, croplands, pastures) than in
570 natural habitats (forests, grassland–shrublands) in 2000, including only sites
571 with a primary habitat covering ≥50% of the area (N = 4,288 assemblages).
572 Fixed effects included primary habitat, habitat heterogeneity (Shannon index),
573 latitude, and elevation, with quadratic terms and interactions initially tested and
574 only significant terms retained; route was included as a random intercept.
575 Temporal changes in functional diversity were examined across 5,688
576 assemblages over 23 years using a within–between decomposition approach to
577 separate within-site (temporal) from between-site (spatial) effects of land-use
578 intensification[39], controlling for latitude, habitat heterogeneity, and elevation.
579 Temporal autocorrelation was modelled with a first-order autoregressive
580 structure (AR(1)), and alternative models considered lagged, cumulative, and
581 non-linear effects. Finally, we measured functional stability as the inverse of
582 the coefficient of variation (1/CV), a widely used measure in studies of the
583 diversity–stability relationship[57], and modelled it as a function of land-use
584 disturbance (% cover of each land-use type), functional redundancy, habitat
585 heterogeneity, and elevation, with route as a random effect. We focused on
586 study sites monitored for at least 15 years and that had suffered minimal land-
587 use change during the 23 years of study (<5% change in urban, cropland, or
588 pasture cover; N = 3974 sites). Model assumptions were checked in all cases to
589 ensure validity. To examine the direct and indirect effects of land use and
590 community properties on functional stability, we used piecewise structural
591 equation modeling in the *R* package piecewiseSEM[58], which allows inclusion
592 of mixed-effects models to account for clustered data structures. Specifically,
593 we fitted linear mixed-effects models for each endogenous variable, including
594 random intercepts for route to account for spatial clustering. The model
595 included all plausible paths based on ecological theory, linking land-use

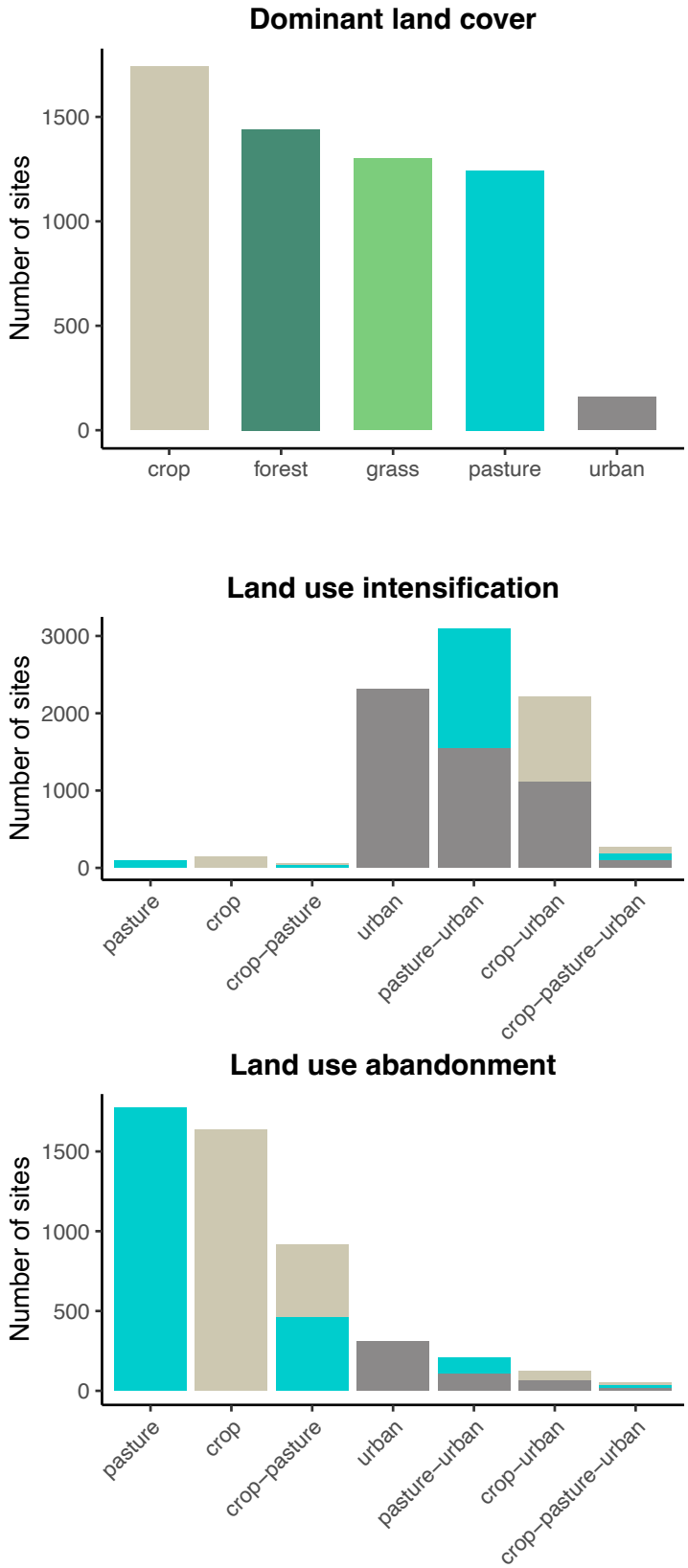
variables (Urban, Crop, Pasture, Heterogeneity) to community properties (functional redundancy, species richness of generalists and habitat heterogeneity) and, ultimately, to functional stability.

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Extended Data Figure Legends



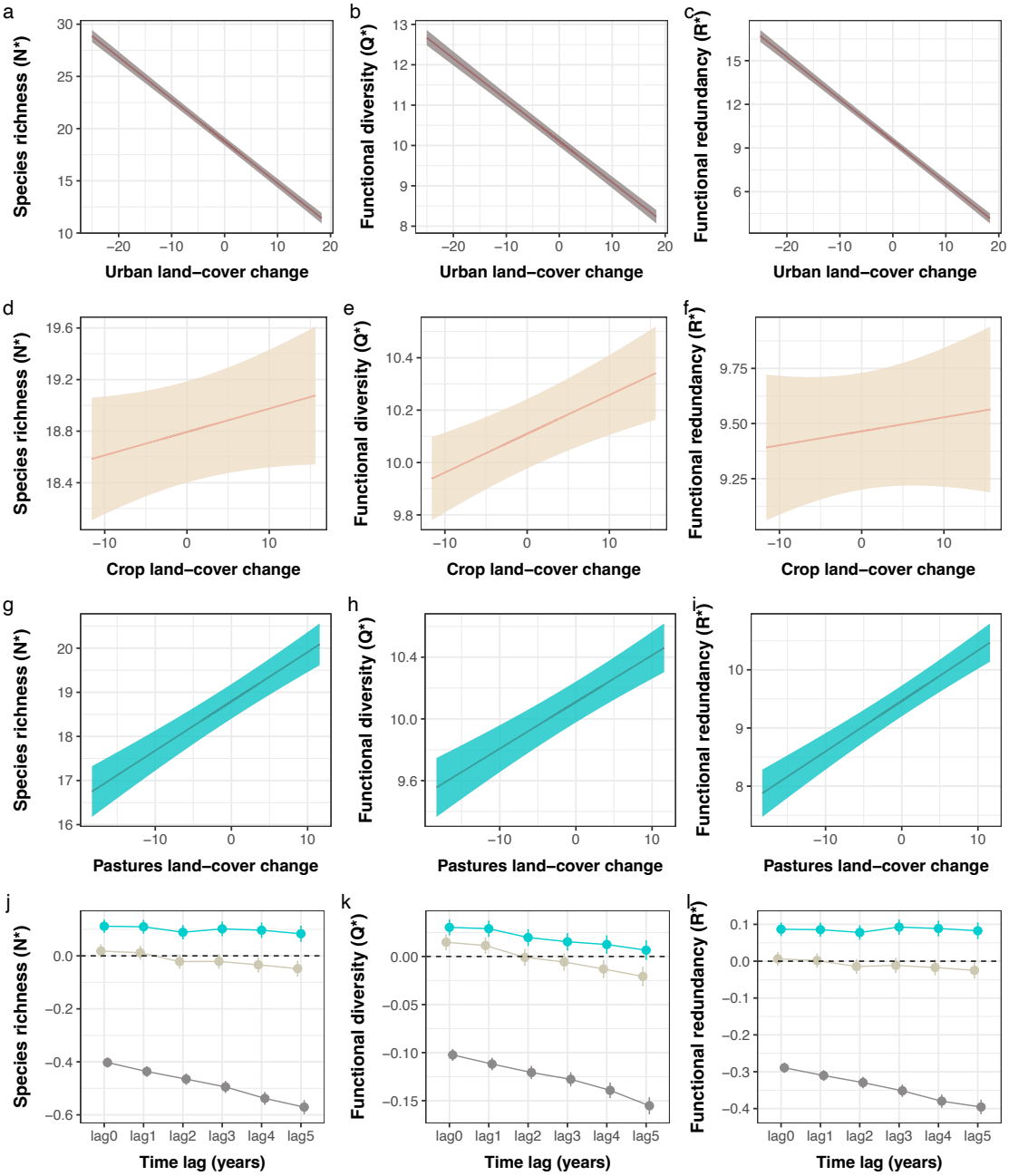
Extended Data Fig 1: Effect of land use intensification on spatial variation in species richness, functional diversity, and functional redundancy. Plots represent the among-effects predictions of the models.



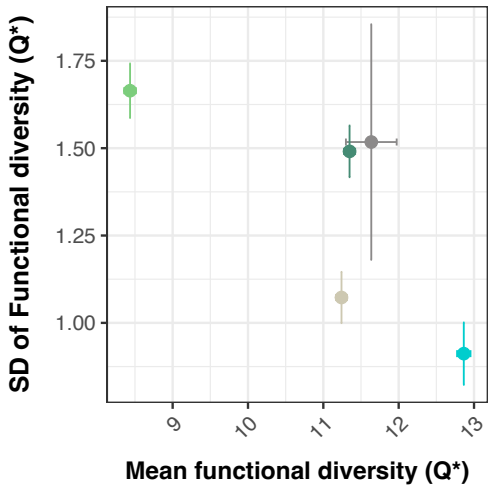
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643 **Extended Data Fig 2: Dominant land cover/use and land-use changes (either**
644 **intensification or abandonment) across the studied sites in the United States.** The
645 proportion of each site occupied by urban areas, crops, pastures, forests, and grasslands
646 (including shrublands) for all studied years was extracted from USGS (2024). The dominant

land cover/use for each site was identified as the category occupying the largest pixels proportion. To assess land-use changes over time, we modeled nonlinear temporal trajectories of crops, pastures, and urban areas using generalized additive models (GAMs; Methods). The direction of each land-use change driver was determined from the mean first derivative of the fitted smooth: positive values indicate increasing human land use (intensification), negative values indicate decreasing land use (abandonment), and values near zero indicate no substantial change.



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671 **Extended Data Fig 3: Impact of species extinctions driven by land use change (within**
672 **effect) on functional diversity**.
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680 **Extended Data Fig 4: Differences across land cover types in the mean and standard**
681 **deviation (SD) of functional diversity over years.**
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Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SoletalNatureSupplementaryInformation.pdf