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Economic growth and bird species richness in Germany

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Abstract

We examine the relationship between economic growth and observed bird species richness in Germany using county-level panel data for 2009–2018. The controlled specifications cover 395 counties. A 1% increase in total county GDP is associated with a 0.17–0.20% decline in species richness in the baseline models. The association remains negative across 32 alternative control configurations and in a Poisson framework. Quantile regressions indicate a stronger negative association at the lower end of the conditional species-richness distribution, with no statistically significant association at the upper quantiles. Trait analyses show larger negative coefficients for farmland birds and species classified as threatened or on the watchlist. A quadratic specification yields an inverted U-shaped relationship, rather than the U-shape consistent with an environmental Kuznets curve for environmental quality. Agricultural land share is associated with a more negative GDP coefficient, particularly for farmland birds. Conservation area share is positively associated with species richness in baseline models, but its interaction with GDP is not statistically significant. Evidence linking GDP to year-to-year species disappearances is weak and specification-dependent. These observational findings identify associations and do not establish causal effects.

Introduction

The relationship between economic growth and biodiversity is a central concern in environmental economics. Cross-country evidence indicates that GDP growth is associated with declining species richness[1,2], and recent work using causal identification finds a similar pattern within national borders[3]. The expectation that this relationship reverses at higher income levels, as suggested by the environmental Kuznets curve, has not been supported empirically for biodiversity[2,4]. Existing evidence is dominated either by global cross-sectional studies[1,2] or by single-country panels outside Europe (for the United States)[3]. Granular county-level panel evidence for Europe, where conservation and agricultural policy are largely shaped at the European Union level, remains scarce[5–7].

We address this gap using German county-level panel data for 2009–2018, with 395 counties. Germany provides an informative high-income European setting in which to examine whether the relationship between total economic activity and bird species richness becomes less negative at higher levels of county GDP. Germany's temperate climate and agricultural landscapes also make it relevant to wider European conservation debates, although the findings need not generalize to other countries. Current debates are shaped by the EU Biodiversity Strategy for 2030, the Common Agricultural Policy, and the EU Nature Restoration Law[8–10]. The strategy and restoration law postdate our observation period. Our analysis provides historical evidence relevant to these debates rather than an evaluation of those policies. Repeated observations allow us to exploit within-county variation while examining potential reporting bias.

A growing literature documents adverse effects of economic activity on biodiversity. Asafu-Adjaye[1] examines 100 countries and finds that economic development is associated with biodiversity loss, with the agricultural sector contributing particularly strongly to this relationship. Sol[2] studies extinction rates across 538 global regions using IUCN Red List data and reports a positive association between GDP per capita and expected extinction rates after accounting for population density, which is consistent with a negative relationship between economic development and biodiversity and inconsistent with an environmental Kuznets curve.

Liang et al.[3] use national military buildups as exogenous shocks to local economic activity and find that economic production reduces species abundance, species diversity, and ecosystem stability across ecological observation sites in the United States between 1960 and 2015, with air pollution accounting for roughly one third of the total effect. Evidence from Europe points to agriculture as an important mechanism. Reidsma et al.[11] document low ecosystem value in intensively used agricultural lowlands across 100 European regions, and Jerrentrup et al.[12] show that intensified maize cultivation negatively affects farmland birds in Lower Saxony. Overall, these studies suggest that economic activity can affect biodiversity both through aggregate production pressure and through land use intensity, yet granular regional panel evidence for Europe remains limited.

Identifying the determinants of species richness decline is essential for effective conservation policy. This is particularly important because the threshold at which species loss becomes intolerable for ecosystem functioning remains unknown[13]. Biodiversity and climate stability both have public good characteristics, since

their benefits are shared broadly and cannot easily be limited to those who pay for their protection. Private markets therefore provide insufficient incentives to preserve biodiversity, much as they underprovide climate mitigation[14]. Understanding how economic activity, land use, and conservation interact is therefore central to designing policies that protect species richness while economic development continues.

Urbanization is another important pathway through which economic development can affect biodiversity. McDonald et al.[15] project that urban expansion through 2030 will reduce natural areas in many ecoregions and bring urban land closer to protected areas, thereby increasing pressure on rare species. More broadly, McDonald et al.[16] review the literature on urban growth and biodiversity and conclude that urbanization tends to disadvantage sensitive and endemic species, while some generalist species can benefit from urban habitats. Climate change adds a further source of pressure by increasing heat stress, drought risk, and environmental variability. In Europe, projections indicate more winter precipitation in central regions and earlier and longer droughts in southern regions[17]. Such changes can affect biodiversity at multiple levels by altering habitats, forcing migration, reducing genetic diversity, and increasing extinction risk[18]. A review by Nunez et al.[19] projects average losses of 14% of originally occurring local species and 35% of climatically suitable area under a 1–2 °C increase in global mean temperature. These metrics do not include potential gains from newly arriving species. Beyond climate change and urbanization, land management practices, especially in managed forests, play a critical role in shaping regional biodiversity outcomes.

Land management and conservation policy shape how these pressures translate into local biodiversity outcomes. Forests cover roughly one third of Germany and provide important ecosystem services, but most forest areas are managed, and intensive management can reduce ecosystem service provision[20]. Protected areas are often associated with higher biodiversity, but this association is difficult to interpret causally because protected status is frequently assigned to places that are already biodiverse or less exposed to development pressure[21]. This distinction is important for our analysis. We therefore distinguish between the level association of conservation areas with species richness and their potential to moderate the relationship between GDP and species richness.

Our contribution is to provide county-level panel evidence for Germany that evaluates the relationship between economic activity and biodiversity across several empirical dimensions. We document a robust negative association between economic growth and bird species richness. A 1 percent increase in county-level GDP is associated with a 0.17 to 0.20 percent decline in species richness. This relationship is stable across a specification curve of 32 alternative control configurations and remains visible across the conditional distribution of species richness in panel quantile regressions. We also examine the shape associated with the environmental Kuznets curve hypothesis by including a quadratic term in total county GDP. Because species richness measures environmental quality rather than degradation, an environmental Kuznets curve would appear as a U-shape. We find the opposite, an inverted U: species richness rises with GDP only in counties with the lowest total GDP, and the turning point lies in the lower part of the observed logged GDP distribution, between the 10th and 25th percentiles. Above it, the marginal association between GDP and species richness is negative.

The heterogeneity analyses indicate that the GDP association is stronger at lower quantiles of the conditional species-richness distribution and becomes statistically indistinguishable from zero at the upper quantiles. Trait-specific coefficients are more negative for farmland birds and for the group comprising threatened and watchlist species. These patterns suggest heterogeneity across ecological groups. Evidence for a relationship between GDP and year-to-year disappearances from the county observation record is weak and specification-dependent: only the random-effects Tobit specification yields a positive coefficient weakly significant at the 10% level.

Interaction models identify agricultural land share as a potential moderator of the GDP–species richness relationship. The GDP coefficient is more negative where agricultural land share is higher, with clearer evidence for farmland birds. Conservation area share is positively associated with species richness in the baseline models, but its interaction with GDP is not statistically significant. Consistent with the concern about selection into protected status examined by Earle Grupp et al.[22], the positive level association should not be interpreted as evidence that protected-area designation causally offsets biodiversity pressures associated with economic growth.

Results

Table 1 reports baseline estimates of the relationship between county GDP and observed bird species richness. Model 1 includes year fixed effects but no county fixed effects or additional controls. A 1% increase in GDP is associated with a 0.17% decrease in species richness, significant at the 5% level.

Model 2 adds county fixed effects, sector controls, and the number of reporting gardens. The GDP coefficient remains negative and increases in magnitude to −0.201, significant at the 1% level. The garden-count coefficient is positive and statistically significant, consistent with greater observation effort increasing the number of species detected.

The agriculture-sector employment control is also negatively associated with species richness in model 2, with a coefficient of −6.687. This variable is a scaled employment measure rather than an unadjusted sector employment share, as explained in the Methods and Supplementary Table S3.

Table 1. Baseline relationship between log species richness and log GDP, 2009–2018

Dependent variable: Ln(Number of species)	**Model 1**	**Model 2**	**Model 3**	**Model 4**
Ln(GDP)	−0.171**	−0.201***	−0.174**	−0.179**
	(0.0818)	(0.0758)	(0.0742)	(0.0728)
Number of gardens	-	0.00174***	0.00174***	0.00174***
		(0.000122)	(0.000126)	(0.000126)
Agricultural land share	-	-	-	−0.399
				(0.366)
Traffic area share	-	-	-	0.217
				(0.521)
Scaled employment in agriculture (A)	-	−6.687***	−5.742***	−5.484***
		(1.191)	(1.278)	(1.315)
Mean evapotranspiration	-	-	−0.000584***	−0.000579***
			(0.000166)	(0.000166)
Median soil moisture	-	-	0.00157***	0.00159***
			(0.000478)	(0.000478)
Annual precipitation	-	-	2.05e−05	2.09e−05
			(3.45e−05)	(3.45e−05)
Mean temperature	-	-	0.0115***	0.0113***
			(0.00349)	(0.00353)
Log maximum temperature	-	-	−0.335	−0.341
			(0.324)	(0.323)
Conservation area (%)	-	-	0.0205*** (0.00516)	0.0206*** (0.00515)
Observations	3,922	3,892	3,883	3,883
R-squared	0.230	0.320	0.340	0.341
Counties	398	395	395	395
Year fixed effects	Yes	Yes	Yes	Yes
County fixed effects	No	Yes	Yes	Yes
Sector controls	No	Yes	Yes	Yes
Climate, land-cover and demographic controls	No	No	Yes	Yes

Note. Standard errors clustered at the county level in parentheses; *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$. Model 1 includes year fixed effects only. Model 2 adds county fixed effects, sector controls and the number of reporting gardens. Models 3 and 4 add the full control vector X. Model 4 also includes agricultural and traffic area shares. Only selected control variables are shown; Supplementary Table S4 reports all control variables. The letters (A–T) refer to the official classification of the industry sectors (Supplementary Table S3)

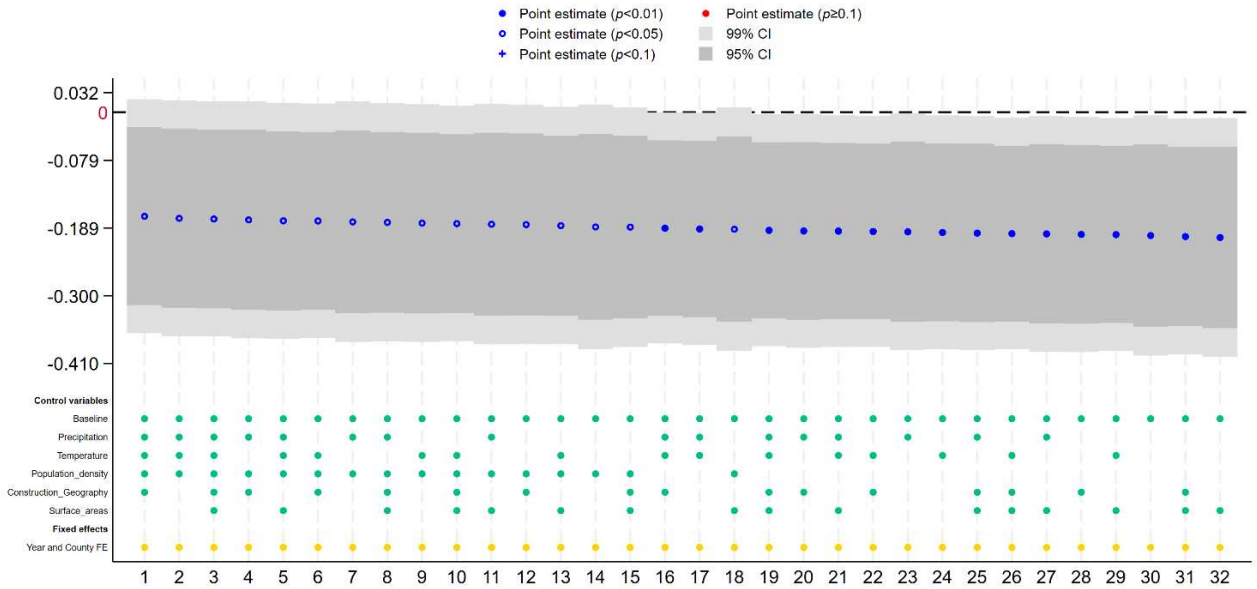
Models 3 and 4 add the full set of control variables. The GDP coefficient remains negative and statistically significant. A 1% increase in GDP is associated with a 0.17% decrease in species richness (model 3), consistent with the baseline results. Several control variables are consistently significant across specifications. Mean evapotranspiration is negatively associated with species richness, while median soil moisture is positively associated with species richness. Average temperature is positively associated with species richness,

whereas logged maximum temperature is not statistically significant. Conservation area share is positive and statistically significant in models 3 and 4, where it is included.

Agricultural land share and traffic area share are excluded from the baseline specification due to collinearity with sectoral employment variables. Including these variables in alternative specifications (model 4) does not affect the magnitude or significance of the GDP coefficient, which remains stable and closely aligned with the baseline estimates.

We assess the robustness of the GDP coefficient using a specification curve approach following Gao et al.[23]. Figure 1 reports estimates from all combinations of control sets applied to the baseline specification. The GDP coefficient remains consistently negative across specifications and statistically significant in the majority of cases.

Figure 1. GDP coefficients across alternative control specifications



Notes: The upper panel reports coefficients on log GDP; in the log–log model, these are elasticities of species richness with respect to GDP. The horizontal axis indexes specifications. Blue dots, blue circles, blue crosses, and red dots denote significance levels. Green dots in the lower panel identify the included control groups, and yellow dots indicate county and year fixed effects.

As an additional robustness check, we re-estimate the models using a Poisson regression framework. Supplementary Fig. S1 presents the corresponding specification curve. The direction and overall pattern of the GDP coefficient remain consistent with the main results, although statistical significance is reduced in some specifications.

Non-linearity and the environmental Kuznets curve

Table 2 reports the estimates of the quadratic specification examining the environmental Kuznets curve pattern using total county GDP. The coefficient on logged GDP is positive and statistically significant, while the squared term is negative and statistically significant, indicating a concave, inverted U-shaped relationship between GDP and species richness. Since species richness measures environmental quality, this shape is the opposite of the U-shape that an environmental Kuznets curve would imply. The implied turning point occurs

at log GDP equal to 7.82. This value lies within the reported range in the estimation sample (6.82 to 11.68), in the lower part of the distribution between the 10th and 25th percentiles, while the sample mean is 8.48.

In economic terms, this implies that for counties at the lower end of the GDP distribution, below the turning point, a 1% increase in GDP is associated with a small increase in species richness. Above the turning point, which applies to the large majority of county-years in the sample, a 1% increase in GDP is associated with a decrease in species richness.

Table 2. Quadratic GDP specification and environmental Kuznets curve test (Eq. 2)

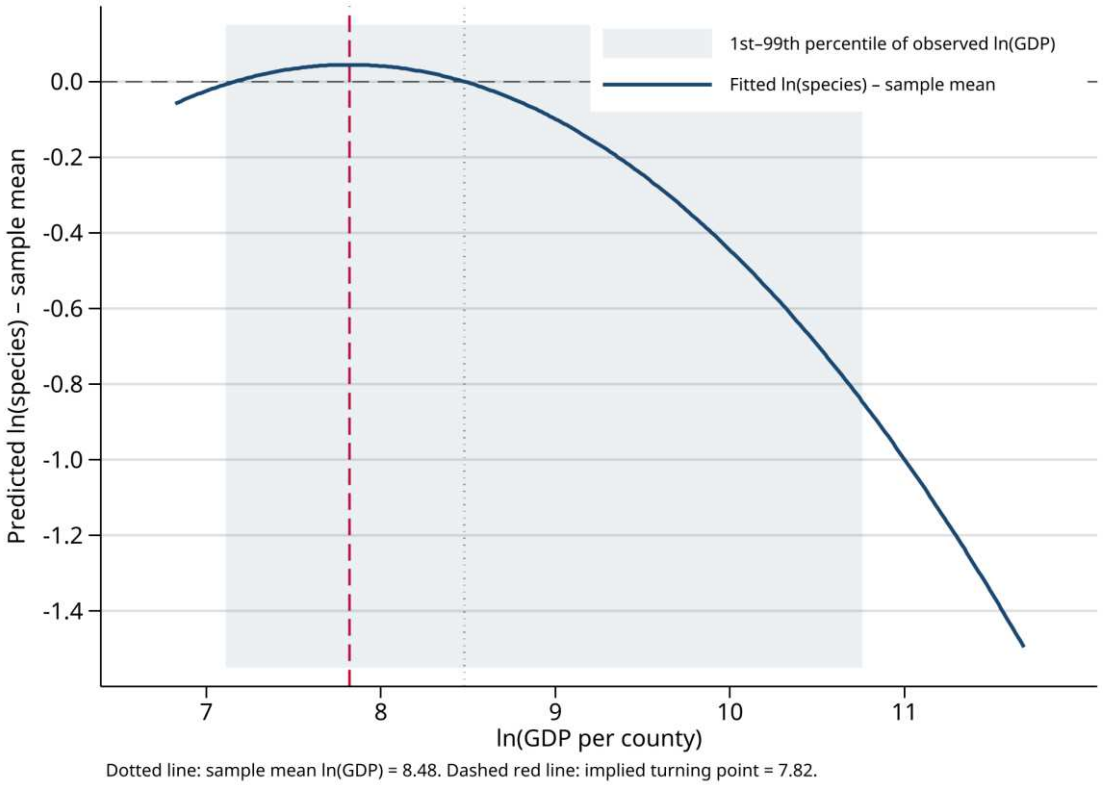
Dependent variable: **Logged Number of Species**	**(1)** **EKC Specification**
Ln(GDP)	1.613*** (0.382)
$Ln(GDP)^2$	-0.103*** (0.0222)
Observations	3,883
Number of counties	395
R-squared	0.350
Year FE	Yes
County FE	Yes
Controls	Yes

Notes: Two-way fixed-effects regression of log species richness on log GDP and $(\log GDP)^2$ with the full control vector X. The implied turning point in log GDP is $-\beta_1 / (2\beta_2) = 7.82$, within the reported estimation-sample log-GDP range (6.82–11.68) and between its 10th and 25th percentiles. Standard errors clustered at the county-level in parentheses. *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$.

Figure 2 illustrates the fitted relationship between GDP and species richness across the observed range of the data. The curve rises only at the lower end of the distribution and slopes downward beyond the turning point, over most of the empirical range. The shape is therefore the opposite of an environmental Kuznets curve: the fitted relationship remains negative at higher levels of total county GDP. This does not directly test the

relationship with income per person. This result is consistent with Sol[2] and Mills and Waite[4], who also do not find evidence supporting an environmental Kuznets curve for biodiversity.

Figure 2. Fitted ln(species) curve from the quadratic specification (Eq. 2), expressed as deviation from the value at the sample mean of ln(GDP)

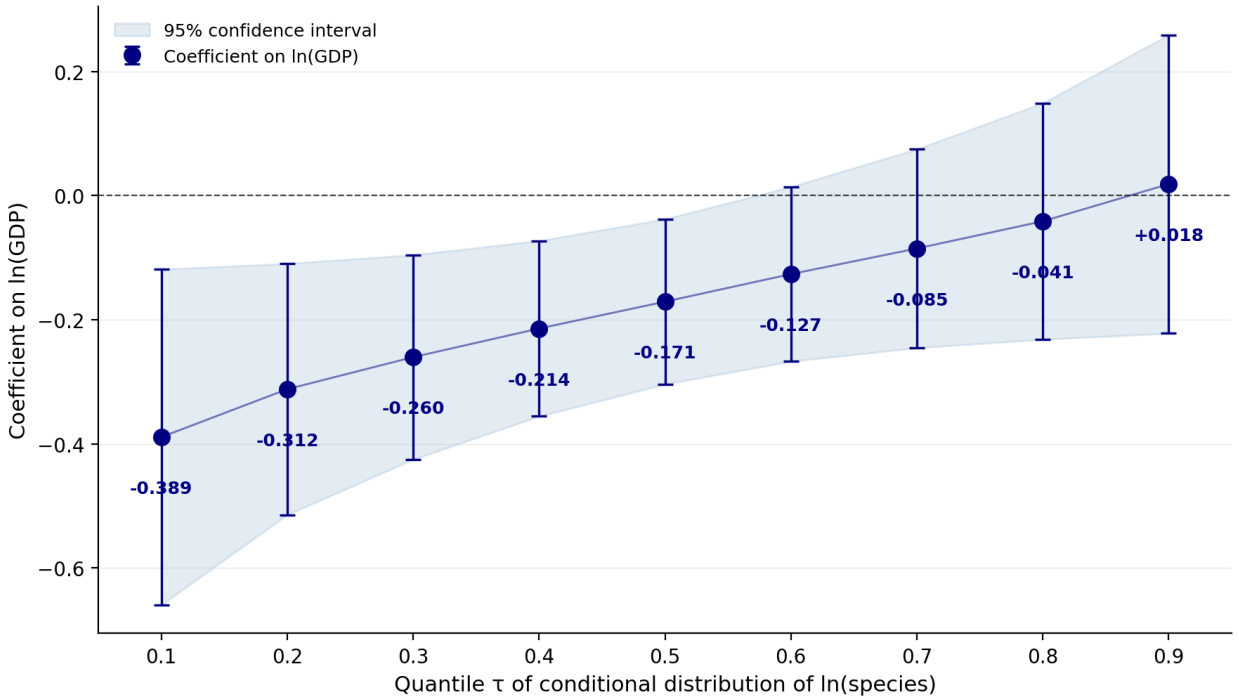


Notes: The curve plots the fitted relationship $\beta_1 \cdot \ln(GDP) + \beta_2 \cdot (\ln GDP)^2$ minus its value at the sample mean of ln(GDP), using the estimates from Table 2. The shaded band marks the 1st–99th percentile of the empirical ln(GDP) distribution; the dotted vertical line marks the sample mean (8.48) and the dashed crimson line marks the implied turning point (7.82). The curve declines beyond the turning point, over most of the empirical support of ln(GDP).

Distributional heterogeneity

We estimate Eq. (3) at quantiles from 0.1 to 0.9 in increments of 0.1 to examine how the GDP coefficient varies across the conditional distribution of species richness. Figure 3 reports the estimated coefficients with 95% confidence intervals.

Figure 3. Panel quantile regression coefficients on log GDP across the conditional distribution of log species richness



Notes: Each point is the estimated coefficient on log GDP from Eq. (3) at the indicated quantile τ of the conditional distribution. Vertical bars are 95% confidence intervals; the shaded band traces the 95% CI continuously. Numeric values (and significance levels) are reported in Supplementary Table S5. The dashed horizontal line marks zero.

Supplementary Table S5 provides the corresponding numerical values. As depicted in Figure 3, the GDP coefficient is most negative at the lower end of the distribution, with a value of −0.39 at the 0.1 quantile, and decreases in magnitude steadily as the quantile increases. The coefficient remains statistically significant at the 5% level up to the median and at the 10% level at the 0.6 quantile, and becomes statistically indistinguishable from zero from the 0.7 quantile onward. Overall, the negative association between GDP and species richness is strongest at the lower quantiles of the conditional species-richness distribution and weakens toward the upper quantiles.

Trait heterogeneity and disappearance dynamics

Table 3 reports GDP coefficients estimated separately for the eight trait subgroups. The magnitude of the GDP coefficient varies systematically across groups. For threatened species, a 1% increase in GDP is associated with a 0.243% decrease in species richness, compared to a 0.149% decrease for non-threatened species, implying that the effect for threatened species is approximately 1.6 times larger. For farmland birds, a 1% increase in GDP is associated with a 0.356% decrease in species richness, compared to a 0.133% decrease for non-farmland species, indicating a substantially larger effect for species associated with agricultural habitats. For migratory species, a 1% increase in GDP is associated with a 0.214% decrease in species richness, while for sedentary species the corresponding effect is a 0.147% decrease, indicating broadly similar responses across these groups. For insectivores, a 1% increase in GDP is associated with a 0.116% decrease in species richness, while for non-insectivores the corresponding effect is a 0.209% decrease and statistically significant, indicating that the GDP association is not concentrated in insectivorous species. In total, the results indicate

that the negative GDP–species richness relationship is concentrated in specific subsets of species, particularly threatened species and species associated with agricultural habitats.

Table 3. GDP coefficients by trait subgroup (Eq. 4)

GDP coefficient by trait group	**(1)**	**(2)**	**(3)**	**(4)**	**(5)**	**(6)**	**(7)**	**(8)**
	Migratory	Sedentary	Insectivores	Non-insectivores	Farmland birds	Non-farmland	Threatened/ watchlist	Other categories
Ln(GDP)	-0.214** (0.0999)	-0.147** (0.0647)	-0.116 (0.0764)	-0.209*** (0.0802)	-0.356*** (0.119)	-0.133* (0.0710)	-0.243** (0.111)	-0.149** (0.0716)
Observations	3,883	3,883	3,883	3,883	3,883	3,883	3,883	3,883
R-squared	0.227	0.356	0.222	0.347	0.154	0.346	0.127	0.360
Number of counties	395	395	395	395	395	395	395	395
County FE	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Year FE	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Controls	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes

Notes: Each column is a separate two-way fixed-effects regression with ln(S + 1) as the dependent variable, where S is the trait-subgroup species count, and the full control vector X. Migratory and farmland classifications follow Bauer et al.[24], Gregory et al.[25], and BTO BirdFacts. The threatened/watchlist group includes German Red List categories 1–3 and V; category V denotes the watchlist[26]. The complementary group excludes these categories. Standard errors clustered at the county-level are in parentheses. *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$.

Supplementary Table S6 reports four models of observed species disappearances: fixed-effects Poisson regression for the count, a linear probability model for any disappearance, a model using the inverse hyperbolic sine of the count, and a random-effects Tobit model left-censored at zero. None yields a GDP coefficient significant at the 5% level. The Tobit coefficient is positive and marginally significant at the 10% level (0.380, $p \approx 0.09$), while the other estimates are not statistically significant. This weak, specification-dependent evidence does not provide robust support for a GDP–disappearance association and cannot establish whether changes in richness reflect gradual or discrete processes.

Interactions with agricultural land and conservation area shares

Table 4 examines the association between GDP and species richness. The interaction between GDP and agricultural land share is negative and statistically significant, indicating that the decline in species richness associated with economic growth becomes stronger as the share of agricultural land increases. In more agriculture-intensive counties, the same increase in GDP is therefore associated with a larger loss in species richness.

In contrast, conservation areas do not alter this relationship. Although conservation area share is positively associated with species richness in levels, its interaction with GDP is statistically insignificant. This indicates that conservation areas do not mitigate the negative association between economic activity and species richness, even in regions with higher levels of protection.

Table 4. Mechanism interactions: GDP × agricultural land share and GDP × conservation share (Eqs. 6 and 7)

Mechanism interactions	**(1)**	**(2)**	**(3)**
	Baseline	Log (GDP) x Agri	Log (GDP) x Conservation
Ln(GDP)	-0.174** (0.0742)	-0.0385 (0.112)	-0.176** (0.0859)
Agricultural land share		2.008 (1.470)	
Ln(GDP) × Agricultural land share		-0.302* (0.179)	
Conservation area (%)			0.0195 (0.0198)
Ln(GDP) × Conservation area (%)			0.000135 (0.00238)
Observations	3,883	3,883	3,883
R-squared	0.340	0.342	0.340
Number of counties	395	395	395
County FE	Yes	Yes	Yes
Year FE	Yes	Yes	Yes
Controls	Yes	Yes	Yes

Notes: Column 1 is the baseline (Eq. 1) for reference. Column 2 estimates Eq. (6), interacting log GDP with the share of agricultural land. Column 3 estimates Eq. (7), interacting log GDP with the share of conservation area. All specifications include the full control vector X, county and year fixed effects. Standard errors clustered at the county-level in parentheses. *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$.

Table 5 estimates the agricultural interaction separately for farmland birds, insectivores, and sedentary species. Because the model includes an interaction between log GDP and agricultural land share, the coefficient on log GDP alone should not be interpreted as the overall GDP effect. Instead, the marginal GDP association depends on the agricultural land share of the county. For farmland birds, the interaction between log GDP and agricultural land share is negative and statistically significant at the 5% level. The coefficient of −0.648 implies that the GDP association becomes substantially more negative as agricultural land share increases. At the sample mean agricultural land share of approximately 0.46, a 1% increase in GDP is associated with roughly a 0.35% decrease in farmland bird richness. This is considerably larger than the average GDP association estimated for total species richness, indicating that farmland birds are especially sensitive to GDP growth in agriculture intensive counties.

For sedentary species, the interaction is also negative and statistically significant at the 10% level. At the sample mean agricultural land share, a 1% increase in GDP is associated with roughly a 0.15% decrease in sedentary species richness. This suggests that the agricultural channel is also visible for species whose local populations are more directly tied to county level habitat conditions. For insectivores, the interaction coefficient is negative but statistically insignificant. At the sample mean agricultural land share, the implied GDP association is also negative, but the estimate is less precise. We therefore do not interpret the insectivore result as evidence of a distinct agricultural moderation effect.

Overall, Table 5 indicates that the agricultural channel is strongest for farmland birds and also present for sedentary species, while the insectivore specification does not provide statistically clear evidence of additional

moderation. Among these subgroup models, the clearest evidence of agricultural moderation is for farmland birds. Evidence for sedentary species is weaker, and the insectivore interaction is not statistically significant.

Table 5. Agricultural-channel interaction (Eq. 6) by trait subgroup

Agri mechanism by trait group	**(1)**	**(2)**	**(3)**
Dependent Variables:	Farmland x agri	Insectivores x agri	Sedentary x agri
Ln (GDP)	-0.0511 (0.183)	-0.0349 (0.114)	-0.0154 (0.100)
Agricultural land share	5.390** (2.375)	1.039 (1.402)	2.134 (1.431)
Ln(GDP) × Agricultural land share	-0.648** (0.286)	-0.186 (0.172)	-0.287* (0.170)
Observations	3,883	3,883	3,883
R-squared	0.156	0.223	0.357
Number of counties	395	395	395
County FE	Yes	Yes	Yes
Year FE	Yes	Yes	Yes
Controls	Yes	Yes	Yes

Notes: Each column estimates the agricultural interaction in Eq. (6) for the indicated trait subgroup. The GDP coefficient alone is evaluated at zero agricultural land share; the marginal GDP association at any other share must also include the interaction term. All specifications include the full control vector X and county and year fixed effects. Standard errors clustered at the county-level are in parentheses. *** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$.

Reporting bias and observation effort

The negative association between GDP and bird species richness persists when we allow observation effort to enter nonlinearly. Replacing the continuous garden-count control with indicators for bands of 50 reporting gardens yields a GDP coefficient of −0.183, significant at the 5% level. Using bands of 10 reporting gardens per 100 km² produces a smaller coefficient of −0.127 at the 10% level (Supplementary Table S7). Allowing the GDP coefficient to vary across observation-effort bands further shows that the negative association is not confined to a particular level of reporting effort (Supplementary Table S8). For garden-count bands, coefficients are negative throughout and statistically significant at the 5% level in all but one band containing few observations. For garden-density bands, coefficients are also consistently negative and significant at the 5% level except in the lowest band, which contains approximately 57% of county-year observations. These findings suggest that the negative association is not solely an artefact of the linear observation-effort control.

Discussion

Our analysis reveals a consistent negative association between economic activity, measured by GDP, and bird species richness at the county-level in Germany over the period 2009–2018. Across specifications, a 1% increase in GDP is associated with a decline in species richness of approximately 0.17 to 0.20%, and this relationship remains after accounting for fixed effects, control variables, and alternative model specifications. This pattern is consistent with a growing body of evidence linking economic development to biodiversity loss, documented in cross-country analyses[1,2] as well as within-country studies using causal identification[3]. By providing county-level panel evidence for a high-income European economy, our results extend this literature

to a more granular spatial scale. Exploiting within-county variation over time allows us to complement earlier cross-sectional and national-level studies and to provide a more detailed view of how economic activity is associated with changes in species richness.

The quadratic specification does not support the U-shaped pattern associated with an environmental Kuznets curve for environmental quality. Instead, it yields an inverted U-shape with a turning point between the 10th and 25th percentiles of the reported estimation-sample GDP distribution. The marginal association is negative for the large majority of county-year observations, with no fitted recovery at higher total county GDP. Since the explanatory variable is total GDP rather than GDP per capita, this result concerns the scale of county economic activity and is not a direct test of an income-per-person threshold. It is consistent in direction with Mills and Waite[4] and Sol[2], who do not find support for an environmental Kuznets curve for biodiversity.

The GDP association varies across the conditional species-richness distribution and ecological groups. Quantile regressions yield more negative coefficients at the lower quantiles, with coefficients statistically indistinguishable from zero from the 0.7 quantile onward. Liang et al.[3] report a related pattern in the United States, where the negative association at the lowest biodiversity decile is almost twice the average. Our trait models yield more negative point estimates for farmland birds and threatened/watchlist species. These estimates describe conditional heterogeneity rather than fixed groups of counties, and formal tests would be required to establish differences between subgroup coefficients.

The interaction results are consistent with agricultural land use contributing to heterogeneity in the GDP–species richness relationship, in line with Reidsma et al.[11]. The negative interaction is clearest for farmland birds, while the evidence is weaker for sedentary species and statistically insignificant for insectivores. Jerrentrup et al.[12] likewise link agricultural land-use changes, particularly intensified maize cultivation, to farmland bird trends in Lower Saxony. Our county-level results extend this comparison geographically, but agricultural land share alone cannot identify intensification as a causal mechanism. One possible explanation for the weaker insectivore result is that this feeding group spans different breeding habitats and nesting strategies. A classification by nesting site could help distinguish these responses. Our trait data do not include nesting characteristics, so we leave this extension to future research. The negative agriculture-sector employment coefficient provides additional evidence of an association with agricultural activity.

Conservation area share is positively associated with species richness in the baseline models, whereas its interaction with GDP is statistically indistinguishable from zero. We therefore find no statistically detectable moderation of the GDP association by conservation area share in these specifications. This is compatible with selection into protection: protected areas may be designated in locations that already have high ecological value or face less development pressure. A positive level association consequently need not reflect a causal effect of designation. Earle Grupp et al.[22] examine this selection problem in evaluating protected-area policies in the European Union. Our observational results cannot determine whether particular conservation policies are effective or rule out protective effects that the interaction models estimate imprecisely.

The GDP coefficient remains negative across the baseline specifications after controlling for agricultural activity, weather, land cover, demographic conditions, and reporting effort. Unobserved changes in habitat, infrastructure, or other local conditions may contribute to this conditional association. The estimates do not identify the relative contributions of these factors, and time-varying reporting bias may also remain.

This finding is relevant for the broader debate on decoupling economic growth from environmental pressure. While our analysis does not identify causal mechanisms, the persistence of a negative within-county elasticity of species richness with respect to GDP suggests that such decoupling is not evident in our data. This is consistent with Otero et al.[27], who argue that absolute decoupling of biodiversity pressure from economic growth has not been observed at meaningful scales.

At the same time, our results should be interpreted as conditional associations rather than causal effects. The analysis relies on observational data and a proxy for biodiversity based on bird species richness, which captures only one dimension of ecological change. Liang et al.[3] find that the negative association with economic activity tends to be more pronounced for non-bird taxa than for birds, so estimates based on birds may understate the response of biodiversity more broadly. The use of citizen-science data introduces potential measurement concerns, although the GDP association remains negative when observation effort is controlled for flexibly. Overall, the evidence provides a consistent picture of the relationship between economic activity and species richness at the regional level, while leaving the precise causal pathways open for future research.

Conclusion

This study examines economic growth and observed bird species richness in German counties during 2009–2018. The baseline estimates indicate that a 1% increase in total county GDP is associated with approximately 0.17–0.20% lower species richness. The negative association persists across alternative control specifications, while quantile models show that it weakens toward the upper end of the conditional species-richness distribution. The quadratic total-GDP specification yields an inverted U-shape, with a negative marginal association for most county-year observations, rather than the U-shape associated with an environmental Kuznets curve for environmental quality.

The trait-specific coefficients are more negative for farmland birds and threatened/watchlist species. Interaction models provide evidence of a more negative GDP association at higher agricultural land shares, particularly for farmland birds, but no statistically detectable moderation by conservation area share. The disappearance models provide only weak, specification-dependent evidence of a GDP association and do not identify the process underlying changes in richness. These findings contribute regional evidence from a high-income European setting, but the observational design identifies associations rather than causal effects.

The findings support closer investigation of agricultural land use and its relationship with biodiversity. Evaluating the effectiveness of conservation measures requires designs that identify policy effects directly. The insignificant conservation interaction in this study does not establish that existing protection is ineffective. Future research should examine causal pathways, more detailed ecological traits, and the effectiveness of specific interventions.

Methods

Data

We combine county-level observations for 2009–2018 from several sources. Throughout the paper, "county" refers to the NUTS3 spatial units represented in the analysis, including urban and rural districts. Bird observations come from NABU's citizen-science survey. GDP, employment, and other structural indicators come from German regional statistics. Land-use indicators are provided by the Leibniz Institute of Ecological Urban and Regional Development through the IÖR-Monitor, and weather data come from the German Meteorological Service. The controlled specifications include 395 counties, the number of observations varies with data availability.

Our bird data come from NABU's citizen-science project "Stunde der Gartenvögel" (Hour of Garden Birds). Birds are widely used as biodiversity indicators because they occur across many habitats, respond to environmental change, and are relatively easy to observe and identify. Their extensive monitoring records and public visibility also support their use in conservation assessment[28–31]. Bird monitoring contributes to Germany's assessment of biodiversity and landscape quality[32]. Species richness nevertheless measures only one aspect of biodiversity[33]. Birds also provide ecosystem services, including seed dispersal and the control of insect populations[34]. Bird-based indicators have limitations. Rare species may be poorly represented, and bird mobility and differences among habitats can weaken correspondence with vegetation or other taxonomic groups[28,35]. Indicator selection therefore needs to reflect the ecosystem and question under study[36–39]. We interpret bird species richness as a taxon-specific biodiversity measure rather than a comprehensive assessment of ecosystem condition. Species richness is the number of species recorded, rather than the number of individual birds. This is the biodiversity dimension most directly measured by our dataset. Both ecological conditions and the observation process can affect the recorded count.

Citizen-science projects involve volunteers in data collection and can extend the geographic and temporal coverage available to researchers. Their reliability depends on survey design, identification accuracy, and observation effort. Gardiner et al.[40] document identification-related biases, including overestimation of species richness, whereas Ross and Henkanaththegedara[41] find agreement between citizen-science and field-survey evidence on urban bird communities. Butler et al.[42] also find value in eBird data but report differences across citizen-science methods and geographic settings. Danielsen et al.[43] provide a framework for evaluating citizen participation in biodiversity monitoring. Such programmes can support conservation research over broad areas and long periods[44–46], and Tsujimoto et al.[47] demonstrate that student observations can contribute useful ecological data. These benefits do not eliminate uneven observer coverage or identification error, which we address through fixed effects and observation-effort controls where possible.

NABU's annual Hour of Garden Birds survey asks volunteers to record, for each species, the maximum number of individuals seen simultaneously during one hour on the designated May survey weekend. The number of bird species recorded in each county-year serves as our species-richness measure. The baseline dependent variable is its natural logarithm. The survey records observations from multiple gardens in each

county. Reported participation increased from approximately 19,000 people across 385 counties in 2009 to more than 34,000 people across 395 counties in 2018. Participation is voluntary, so these observations are neither a random sample nor necessarily representative of all habitats. The recurring May survey window improves seasonal comparability but does not eliminate differences in weather, phenology, detection, or observer composition. Citizen-science counts may be biased, including through overestimation of species richness[40], and the direction and magnitude of bias may vary with education, garden size, or available leisure time. We adress the limitation of reporting bias, by applying county fixed effects, which absorb time-invariant components of such differences. Additionally, controls address some time-varying variation, and we apply a non-linear analysis as a robustness check. However, we cannot fully guarantee that the bias is removed and acknowledge this limitation.

More specifically, in our analysis, we focus on species richness rather than bird abundance because the observed number of individual birds within a species depends on the number of reporting gardens (vantage points). Greater reporting effort may also increase the number of species detected. We account for this by controlling for the number of reporting gardens in the baseline specification. In robustness checks, we replace this continuous control with indicators for reporting-effort bands, defined either in increments of 50 gardens or in increments of 10 gardens per 100 km². We additionally allow the GDP coefficient to vary across these bands to assess whether the association between economic activity and species richness differs with observation effort.

We aggregate the weather variables to the county-year level, using annual temperature measures, precipitation, soil moisture, and actual evapotranspiration. Evapotranspiration combines evaporation from soil and plant surfaces with plant transpiration.

The DWD temperature grids encode values in tenths of a degree Celsius; dividing a grid value by 10 converts it to °C. The maximum-temperature series reports annual averages of monthly mean daily maximum air temperatures measured at 2 m above ground[48]. Soil moisture is expressed as a percentage of plant-available water[49]. Precipitation is the annual total in millimetres[50]. The cited evapotranspiration grids encode values in tenths of a millimetre and require division by 10 for conversion to millimetres[51]. These gridded products have a spatial resolution of 1 × 1 km. We use QGIS to calculate county averages and organize the controls into thematic groups covering economic structure, weather, demographics and infrastructure, land cover, and reporting effort. Supplementary Table S1 reports descriptive statistics.

Empirical Strategy

We estimate the within-county relationship between economic activity and bird species richness using a two-way fixed-effects panel model. The baseline specification relates the natural log of observed species richness to the natural log of county GDP and a vector of time-varying county controls:

$$\ln(Species_{it}) = \beta_1 \ln(GDP_{i,t}) + X'_{it}\gamma + \alpha_i + \lambda_t + \varepsilon_{it} \quad (1)$$

where $\ln(Species_{it})$ is the natural log of the number of bird species observed in county i in year t, and $\ln(GDP_{it})$ is the natural log of total county GDP. The log–log form permits an elasticity interpretation, the fixed-effects specification uses within-county variation over time[52]. County fixed effects α_i capture time-invariant differences across counties, such as geography and habitat structure, while year fixed effects λ_t absorb shocks common to all counties, including macroeconomic conditions and common variation in reporting. The control vector X_it is organized into thematic groups capturing time-varying socioeconomic, climatic, land-cover, and observation-effort controls. Standard errors are clustered at the county-level to allow for arbitrary serial correlation.

The coefficient β_1 is interpreted as the elasticity of species richness with respect to GDP. We use total GDP rather than GDP per capita, as the scale of economic activity is central to environmental pressure. The control vector includes variables capturing economic structure, climate conditions, demographics and infrastructure, land cover, and reporting intensity. The sector controls describe the employment structure of each county with seven mutually exclusive sectors that together cover total employment: agriculture (A); mining, energy and water supply (B, D–E); manufacturing (C); construction (F); trade, transport, hospitality and information (G–J); finance, insurance, real estate and business services (K–N); and public and other services (O–T). For each sector, the number of persons employed in the sector at their place of work in the county is divided by the number of employees subject to social security contributions at their place of work and multiplied by the county's employment rate (Supplementary Table S3). Each sector variable is therefore the sector's share of local employment, scaled by a county-specific factor, and the seven variables sum to 0.81 on average rather than to one. Because they do not sum to a constant, no sector has to be omitted as a reference category. All sector variables have variance inflation factors below 4; among all regressors, only the two temperature variables exceed 10. Dropping the share of sectors O–T leaves the GDP coefficient almost unchanged (−0.160, $p = 0.031$). Agricultural land share is excluded from the baseline due to collinearity with sectoral employment shares and is introduced separately in the mechanism analysis.

Robustness and functional form

To assess whether the GDP coefficient is sensitive to the choice of controls, we implement a specification curve following Gao et al.[23]. We hold ln(GDP), fixed effects, and sectoral controls constant, and vary additional control groups across all combinations. This results in 32 alternative specifications. We re-estimate these models using a Poisson pseudo-maximum likelihood framework with high-dimensional fixed effects[53], which retains the count nature of the dependent variable (Supplementary Fig. S1).

We also test the environmental Kuznets curve hypothesis by including a quadratic term in log GDP:

$$\ln Species_{it} = \beta_1 \ln GDP_{it} + \beta_2 (\ln GDP_{it})^2 + X_{it}'\gamma + \alpha_i + \lambda_t + \varepsilon_{it} \quad (2)$$

For an environmental-quality outcome such as species richness, the pattern associated with the environmental Kuznets curve is U-shaped ($\beta_1 < 0$, $\beta_2 > 0$). An inverted U-shape ($\beta_1 > 0$, $\beta_2 < 0$) implies the opposite pattern. In this study, the horizontal axis is total county GDP rather than income per person. The turning point in log

GDP is $-\beta_1 / (2\beta_2)$. We compare it with the empirical estimation-sample GDP distribution to assess whether the fitted reversal occurs within the observed range.

Distributional and trait heterogeneity

To examine how the GDP–species richness relationship varies across the distribution, we estimate panel quantile regressions at quantiles $\tau \in \{0.1, \ldots, 0.9\}$:

$$Q_\tau(\ln Species_{it} \mid \ln GDP_{it}, X_{it}, \alpha_i, \lambda_t) = \beta_1(\tau)\ln GDP_{it} + X'_{it}\gamma(\tau) + \alpha_i(\tau) + \lambda_t(\tau) \quad (3)$$

This specification estimates how the GDP association varies across quantiles of the conditional species-richness distribution. These quantiles do not represent fixed groups of counties.

To examine heterogeneity across ecologically meaningful dimensions, we classify bird species into several trait-based subgroups commonly used in the literature. Farmland species are defined following the European farmland bird indicator, which is widely used to monitor biodiversity in agricultural landscapes[25,54]. The threatened/watchlist group comprises categories 1–3 and V of the German Red List of Breeding Birds[26], which categorizes species according to their conservation status, V denotes the watchlist. This grouping therefore includes both threatened and watchlist species. Migratory and sedentary classifications are based on established ornithological references and species-specific information from Bauer et al.[24] and the British Trust for Ornithology's BirdFacts database. Finally, species are grouped by feeding behavior into insectivores and non-insectivores, based on their primary diet during the breeding season, drawing on ecological trait classifications from standard ornithological sources[24]. These classifications allow us to further examine heterogeneity across ecological characteristics by estimating the baseline model separately for species subgroups:

$$\ln(Species_{it}^k + 1) = \beta_1^k \ln GDP_{it} + X'_{it}\gamma^k + \alpha_i^k + \lambda_t^k + \varepsilon_{it}^k \quad (4)$$

where k indexes trait groups including migratory status, feeding behavior, habitat association, and conservation status. We use $\ln(count + 1)$ because some county-year observations contain zero species in smaller trait groups. The coefficient measures the elasticity of the species count plus one with respect to GDP. The elasticity of the count itself depends on its level, so we compare model coefficients rather than interpret them as exact percentage changes in species richness.

Disappearance dynamics

We construct a county-year disappearance count from consecutive annual observation records. A species contributes one event if it was recorded in a county in year t − 1 but was not recorded there in year t. We sum these events across species:

$$Disappear_{it} = \sum_s 1\{Specie\, s_{s,i,t-1} > 0 \text{ and } Species_{s,i,t} = 0\} \quad (5)$$

This measure describes a disappearance from the citizen-science record, not confirmed biological extinction. Non-detection can reflect ecological change or changes in observation and detection, and the measure does

not distinguish gradual from discrete losses. We estimate four complementary models. First, we estimate a fixed-effects Poisson model for the disappearance count. Second, we estimate a linear probability model for an indicator equal to one if at least one species disappears from the county year observation record. Third, we use the inverse hyperbolic sine of the count, and fourth, a random-effects Tobit model left-censored at zero[55]. All specifications include year fixed effects and the full control vector, and all but the Tobit model include county fixed effects. Because the first sample year has no prior-year observation, the measure is defined from 2010 onward.

Mechanism interactions

To examine potential moderation, we estimate interaction models between GDP and land-use variables. The first specification interacts log(GDP) with agricultural land share:

$$\ln Species_{it+1} = \beta_1 \ln GDP_{it} + \beta_2 A_{it} + \beta_3 (\ln GDP_{it} \times A_{it}) + X_{it}^{-A}\gamma + \alpha_i + \lambda_t + \varepsilon_{it} \qquad (6)$$

where A_{it} is the share of county area in agricultural use, and X_{it}^{-A} denotes the baseline controls excluding the agricultural land share when it enters separately as a moderator. A negative β_3 indicates that the marginal association between GDP and species richness is more negative in counties with higher agricultural land shares.

The second specification interacts GDP with conservation area share:

$$\ln Species_{it+1} = \beta_1 \ln GDP_{it} + \beta_2 C_{it} + \beta_3 (\ln GDP_{it} \times C_{it}) + X_{it}^{-C}\gamma + \alpha_i + \lambda_t + \varepsilon_{it} \qquad (7)$$

where C_{it} is the conservation area share, and X_{it}^{-C} denotes the baseline controls excluding conservation share when it enters separately as a moderator. Since the baseline GDP coefficient is negative, a positive β_3 would indicate that conservation areas attenuate the negative GDP–species richness association. A statistically insignificant interaction provides no statistically detectable evidence of moderation; it does not establish that the true interaction is zero. This distinction is central because protected areas may be located in already biodiverse places, which would generate a positive level association without implying that conservation designation offsets growth-related biodiversity pressure.

Reporting bias robustness

Citizen-science data introduce a specific measurement concern. Counties with higher income or more engaged residents may generate more reports, and a larger number of reporting gardens can increase the probability of observing more species. The baseline model controls for the number of reporting gardens, but this may not fully address the concern if reporting intensity is itself correlated with economic activity.

To assess whether our findings depend on how we account for observation effort, we estimate two additional specifications. These replace the continuous garden count with indicator variables for bands of 50 reporting gardens or bands of 10 reporting gardens per 100 km² of county area. Both specifications allow for a nonlinear relationship between observation effort and observed species richness. All specifications retain county and year fixed effects, accounting for time-invariant differences across counties and common annual shocks, including common changes in reporting effort. We do not additionally normalize garden counts by population, as persistent differences in population size are absorbed by county fixed effects, while changes in population

density are captured by the controls. Similar GDP coefficients across these specifications would provide further evidence that the baseline association is not driven by the way observation effort is modelled.

Data availability

The bird count data are publicly available from NABU's Hour of Garden Birds ("Stunde der Gartenvögel"): https://www.nabu.de/tiere-und-pflanzen/aktionen-und-projekte/stunde-der-gartenvoegel/ergebnisse/15767.html. County GDP and employment data are available from the regional accounts of the German federal and state statistical offices (https://www.statistikportal.de/de/vgrdl) and further structural indicators from the regional database of the statistical offices (https://www.regionalstatistik.de). Land-use data are from the IÖR-Monitor of the Leibniz Institute of Ecological Urban and Regional Development (https://www.ioer-monitor.de), and weather data from the Climate Data Center of the German Meteorological Service (https://opendata.dwd.de/climate_environment/CDC/). The county panel compiled from these sources is available from the corresponding author on reasonable request.

Code availability

The Stata code used for the analysis is available from the corresponding author on reasonable request.

Author contributions

L.F.: conceptualization, data curation, formal analysis, writing – original draft.

N.A.: formal analysis, writing – review and editing.

U.E.: data (NABU bird counts), ecological interpretation, writing – review and editing.

C.H.: supervision, writing – review and editing. All authors approved the final manuscript.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Deepl.com/write, Grammarly and ChatGPT to improve the language and language editing. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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