домінуючий характер змін змінився зі змішаного (34,435 негативних; 66,575 позитивних) на виражено позитивний (11,705 негативних; 88,305 позитивних), що вказує на помітне озеленення міського середовища. Повністю скриптований робочий процес Python/GEE забезпечує відтворювану та масштабовану альтернативу традиційним підходам настільних ГІС для довготривалого моніторингу міської рослинності.

Ключові слова: KNDVI, міська рослинність, просторово-часовий аналіз, Google Earth Engine, Вінниця.

REFERENCES

1. Zhang, Y., Zhang, X., Liu, S., & Cai, W. (2022). Spatiotemporal variation of vegetation NDVI and its climatic driving forces in global land surface. *Polish Journal of Environmental Studies,* 31(4), 3541–3549. https://doi.org/10.15244/pjoes/145063

2. Nowak, D. J., & Crane, D. E. (2002). Carbon storage and sequestration by urban trees in the USA. *Environmental Pollution,* 116(3), 381–389.

3. Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution,* 20(9), 503–510.

4. Tucker, C. J. (1979). Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment,* 8(2), 127–150.

5. Camps-Valls, G., Campos-Taberner, M., Moreno-Martínez, Á., Walther, S., Duveiller, G., Cescatti, A., Mahecha, M. D., Muñoz-Marí, J., García-Haro, F. J., Guanter, L., Jung, M., Gamon, J. A., Reichstein, M., & Running, S. W. (2021). A unified vegetation index for quantifying the terrestrial biosphere. *Science Advances,* 7(9), eabc7447

6. Li, X., Wang, L., Geng, X., & Zhou, W. (2022). Spatiotemporal variation of vegetation NDVI and its climatic driving forces in global land surface. *Polish Journal of Environmental Studies,* 31(4), 3541–3549.

UDC 504.064:591.5:598.2(7)

TEMPORAL TRENDS IN BREEDING BIRD DIVERSITY ACROSS NORTH AMERICA: A LINEAR MIXED-EFFECTS MODEL ANALYSIS

O. S. Mozharovskyi, A. M. Mishchenko

Summary. Long-term biodiversity monitoring data require analytical frameworks that can simultaneously capture continental-scale trends and local variation. We applied linear mixed-effects models (LMMs) to data from the North American Breeding Bird Survey (BBS) spanning 440 survey routes and 24 years (1984–2007) to assess temporal trends in six biodiversity indices – species richness (S), total abundance (N), Shannon entropy (H), and Simpson-based indices (D, 1−D, 1/D) – and to evaluate whether climate (temperature, precipitation) and vegetation (NDVI) can account for the observed trends. Fixed effects in LMMs estimate trends in mean local (alpha) diversity, while random effects quantify heterogeneity among locations (beta diversity). All biodiversity indices showed statistically significant directional trends over the study period. Species richness, Shannon entropy, and evenness-related indices increased moderately, while total abundance declined. Intraclass correlation coefficients (ICC = 0.75–0.96) confirmed that location identity accounted for the dominant share of variance in all indices. Climate and vegetation explained negligible fractions of the temporal trends: adding temperature, precipitation, and NDVI to the models caused no meaningful attenuation of the year coefficient for any index except abundance. LMMs offer substantial advantages over location-by-location regression, including partial pooling of information across sites, formal decomposition of variance between alpha and beta levels, and valid inference under the clustered structure of monitoring data.

Keywords: Breeding Bird Survey; biodiversity monitoring; linear mixed-effects models; alpha diversity; beta diversity; species richness; biotic homogenization; North America; long-term trends; climate effects.

Introduction. Biodiversity underpins ecosystem functioning, resilience, and the services that natural systems provide to human societies [1]. Quantifying how biodiversity changes over time and identifying the environmental drivers of such change are therefore central tasks of contemporary ecology and conservation biology. Yet biodiversity is not a single quantity – it is structured across spatial scales. The framework introduced by [7] distinguishes local (alpha) diversity, the diversity measured at a single site; regional (gamma) diversity, the diversity of a whole landscape or continent; and beta diversity, the variation in species composition among sites that connects alpha to gamma scales.

This multi-scale structure has important consequences for how biodiversity trends are analysed and interpreted. A gamma-level analysis – for example, counting the total number of species observed anywhere in North America in a given year – is insensitive to the most pervasive form of contemporary biodiversity loss: biotic homogenization. When abundant generalist species spread while specialists decline, local communities become impoverished and increasingly similar to one another, even though few species are lost at the continental scale. Monitoring gamma diversity alone can therefore give a misleading picture of ecological health. Trends in mean alpha diversity, by contrast, directly reflect what a typical local community experiences, and variation in those trends across locations (beta diversity dynamics) reveals whether change is spatially homogeneous or concentrated in particular regions or habitat types.

Linear mixed-effects models (LMMs) provide a principled statistical framework for analysing hierarchically structured monitoring data of this kind. When survey locations are measured repeatedly over time, standard regression treats repeated observations within the same location as independent. LMMs resolve this by partitioning variance into within-location and between-location components, yielding fixed effects that describe the average trend across all locations and random effects that quantify location-specific departures from that average. In the context of biodiversity analysis, this maps directly onto the alpha/beta diversity framework: fixed effects characterise alpha diversity dynamics (the typical local community), while the variance of random effects characterises beta diversity (among-location heterogeneity in baselines and trends).

Here we apply LMMs to data from the North American Breeding Bird Survey (BBS), one of the longest-running and most spatially extensive avian monitoring programmes in the world. Our analysis addresses three research questions:

1. Are there significant long-term trends in mean local biodiversity of breeding birds in North America between 1984 and 2007, and do these trends differ among locations (alpha vs. beta diversity dynamics)?
2. What is the structure of spatial heterogeneity – do locations with higher baseline diversity show faster or slower rates of change?
3. Are temperature, precipitation, and vegetation greenness (NDVI) drivers of the observed temporal trends, or do these climatic and phenological variables merely correlate with biodiversity without mediating the trend?

Materials and methods. *The North American Breeding Bird Survey.* The Breeding Bird Survey is a roadside point-count monitoring programme initiated in 1966 and coordinated by the United States Geological Survey (USGS) and Environment and Climate Change Canada [4; 5]. Each survey route consists of 50 stops spaced 0.8 km apart, where a trained observer records all birds seen or heard within a 400 m radius during a 3-minute count. Routes are surveyed once per year during the peak of the breeding season. For this study, we used data from 440 routes distributed across North America, covering the period 1984–2007 (10,247 route–year observations; 19–24 annual records per route).

Biodiversity Indices. For each route and year, we computed six biodiversity indices from species-level abundance counts: species richness (S), total abundance (N), Shannon entropy (H), Simpson's dominance index (D) and its complements ($1-D$, $1/D$). Species richness and abundance characterise the first and zeroth moments of the abundance distribution, respectively. Shannon entropy reflects both richness and evenness, and the Simpson-based indices emphasise the relative dominance of the most abundant species, making them robust to incomplete species detection.

Environmental Predictors. Annual mean temperature (T) and total annual precipitation (pre) at each route were extracted from the Climatic Research Unit gridded dataset CRU TS v4.09 [2]. The Normalized Difference Vegetation Index (NDVI) was calculated from Landsat 4–7 imagery (sensor depending on year), averaged over the 5–8 month growing season for each route location. All predictors were standardised to zero mean and unit standard deviation prior to modelling to facilitate convergence and to make effect sizes comparable across predictors.

Statistical Models and Their Ecological Interpretation. We fitted three LMM specifications. All models were implemented in Python using the statsmodels library [6], with parameters estimated by restricted maximum likelihood (REML).

Model 1: *Y ~ year + (1 + year | location_id)* assessed the global temporal trend in each biodiversity index. The fixed intercept estimates the continental mean baseline of the index (mean alpha diversity); the fixed slope of *year* estimates the average rate of change per year across all 440 routes. The random intercept variance (Group Var) quantifies between-route variation in baseline diversity – the beta-diversity signal. The random slope variance (year Var) quantifies heterogeneity in temporal trends: a large year Var indicates that some routes are increasing while others are decreasing, a signature of spatially heterogeneous change. The covariance between random intercepts and slopes (Group × year Cov) reveals whether routes with higher baseline diversity tend to change faster or slower. The intraclass correlation coefficient ICC = Group Var / (Group Var + Residual Var) measures the proportion of total variance attributable to stable between-route differences.

Model 2: *T ~ year + (1 + year | location_id)* applied the same structure with temperature as the response, to test whether temperature itself exhibited a significant directional trend over the study period. This is a necessary precondition for temperature to mediate biodiversity trends.

Model 3: *Y ~ year + T + pre + NDVI + (1 + year | location_id)* extended Model 1 by adding climate and vegetation predictors as fixed effects. The fixed coefficients of *T*, *pre*, and NDVI describe average associations between these predictors and the biodiversity index, after partialling out the year trend. Critically, if one or more predictors mediate the temporal trend (i.e., if they represent the mechanism by which year affects *Y*), then adding them to the model should attenuate the *year* coefficient relative to Model 1. The absence of such attenuation indicates that the predictor is associated with *Y* but does not explain the trend. This framework corresponds to the Baron–Kenny mediation test, where the indirect (mediated) effect of year on *Y* through predictor *X* equals the product of the year→*X* coefficient and the *X*→*Y* coefficient, and is reflected in the attenuation of the direct year coefficient when *X* is included.

LMMs Versus Location-by-Location Regression. A natural alternative to LMM is to fit a separate OLS regression for each of the 440 routes and then summarise results. This approach has several limitations. First, routes with few observations yield unreliable estimates; OLS cannot borrow strength from the broader dataset. Second, testing for a global trend requires aggregating 440 p-values, which introduces multiple comparison problems even after correction. Third, OLS residuals within a route are temporally autocorrelated, violating the independence assumption and inflating Type I error. LMMs address all three problems: partial pooling shrinks noisy site-specific estimates toward the grand mean; a single model tests the global trend with one coefficient; and the random effects structure accounts for within-route correlation by design.

Results. Temporal Trends in Mean Local Biodiversity (Model 1). Table 1 presents results for Model 1 fitted separately to temperature and to each of the five biodiversity indices. In all cases the model converged and the global trend in year was statistically significant.

Table 1

Fixed and random effect parameter estimates from Model 1 (Y ~ year + (1 + year | location_id)) fitted to temperature (T) and five biodiversity indices. All predictors are standardised. Standard deviations (SD) of random effects and residuals are reported in place of variances. ICC = intraclass correlation coefficient for the random intercept.

***** $p < 0.001$, * $p < 0.05$, ns = not significant**

	T	***S***	***N***	***H***	**1−*D***	***1/D***
Intercept	10.937***	54.668***	818.186***	3.249***	0.933***	18.653***
year (fixed slope)	0.175***	0.736***	−14.455*	0.028***	0.003***	0.379***
Group SD (intercept)	3.213	9.907	323.6	0.348	0.032	6.571
Year SD (slope)	0.063	2.485	123.1	0.078	0.000	1.469
Group × year Cov	−0.066	−0.431	−3414	−0.007	0.000	−1.434
Residual SD	0.670	3.985	173.1	0.130	0.022	2.897
ICC (intercept)	0.958	0.861	0.778	0.876	0.754	0.837

Species richness increased on average by 0.74 species per standardised year unit, and total abundance declined by approximately 14.5 individuals. Shannon entropy and evenness-based indices ($1-D$, $1/D$) increased significantly, indicating that the relative dominance of the most abundant species decreased over time – consistent with a reduction in the numerical dominance of a few highly abundant species (e.g., certain sparrow populations) and a redistribution of abundance across species that produces higher evenness without necessarily adding new species to local communities.

Alpha diversity dynamics. The fixed intercepts reflect the continental mean of each index: 54.7 species per route, 818 individuals, Shannon $H = 3.25$. The positive year slopes for all indices except N indicate a consistent increase in mean local diversity over the 24-year period.

Beta diversity and spatial heterogeneity. The ICC values (0.75–0.96) reveal that between-route differences account for 75–96% of total variance in all indices – far larger than the within-route temporal signal. Routes differ enormously in their baseline diversity, reflecting the breadth of habitats sampled by BBS across North America (boreal forest, grassland, desert, coastal). The random slope variances (year SD = 2.5 for S, 123 for N) are also substantial, confirming that the global trend is highly heterogeneous: some routes show strong increases in richness, others declines. This spatial heterogeneity in trends is a beta-diversity-level finding that a continental-scale or gamma-level analysis would conceal.

Baseline–trend covariance. The Group × year Cov is negative for all biodiversity indices (e.g., −0.43 for S, −3414 for N). This indicates that routes with higher baseline diversity tend to show more negative trends (slower increase or faster decline), while routes with initially lower diversity tend to improve more rapidly. For abundance this suggests that historically abundant communities are declining most steeply, consistent with documented collapses of common-bird populations. For diversity indices the pattern suggests partial regression to the mean, but may also reflect genuine ecological dynamics such as reduced habitat carrying capacity at initially species-rich sites.

Temperature trend (Model 2). The fixed year coefficient for temperature (0.175, $p < 0.001$) indicates a statistically significant warming trend at the continental average. However, the ICC for temperature is extremely high (0.958), meaning that virtually all temperature variance is attributable to stable geographic differences among routes (latitude, altitude). The year SD (0.063) is very small relative to Group SD (3.21), indicating that within-route warming trends are modest and highly variable. After multiple-testing correction across 440 routes, only a handful show individually significant warming trends, consistent with our preliminary OLS screening.

Climate and Vegetation as Drivers of Biodiversity Trends (Models 1–3). Table 2 presents results for Model 3, which adds temperature, precipitation, and NDVI as fixed effects.

Table 2

Fixed and random effect estimates from Model 3
(Y ~ year + T + pre + NDVI + (1 + year | location_id)) fitted to five biodiversity indices.
All predictors are standardised. SD = standard deviation of random effect or residual.
***** p < 0.001, * p < 0.05, ns = not significant**

	S	***N***	***H***	**1−*D***	***1/D***
Intercept	54.667^{***}	818.000^{***}	3.249^{***}	0.933^{***}	18.652^{***}
year (fixed slope)	0.720^{***}	-15.902^{*}	0.028^{***}	0.003^{***}	0.367^{***}
T (temperature)	0.183^{ns}	61.657^{***}	-0.001^{ns}	-0.001^{ns}	0.139^{ns}
pre (precipitation)	0.086^{ns}	-6.121^{ns}	0.003^{ns}	0.001^{ns}	0.075^{ns}
NDVI	0.081^{ns}	-8.917^{*}	0.004^{ns}	0.001^{*}	0.059^{ns}
Group SD (intercept)	9.880	322.1	0.345	0.032	6.526
Year SD (slope)	2.486	123.1	0.078	0.000	1.469
Group × year Cov	−0.460	−3388	−0.007	0.000	−1.429
Residual SD	3.985	172.7	0.130	0.022	2.898
ICC (intercept)	0.860	0.777	0.875	0.748	0.835

Mediation test. The central diagnostic is the change in the fixed year coefficient between Model 1 and Model 3. For all indices, this change is negligible: the year slope for S shifts from 0.736 to 0.720 (−2.2%); for N from −14.46 to −15.90 (an increase in magnitude of 10%, in the wrong direction for mediation); for H and the Simpson indices the changes are below 1%. This absence of attenuation demonstrates that temperature, precipitation, and NDVI do not mediate the long-term temporal trends in breeding bird biodiversity. Even where year-to-year variation in biodiversity is associated with climate, that association does not account for the directional trend.

Individual predictor effects. Temperature is the only climate variable with a significant fixed effect, and only for total abundance (N: coef = 61.7, $p < 0.001$). This indicates that warmer years are associated with higher bird counts, plausibly through phenological effects on insect availability or overwinter survival, but this within-route interannual temperature signal does not translate into a mediated trend because within-route warming is small relative to the between-route temperature variation. NDVI shows a marginal significant negative effect on N (−8.9, $p = 0.049$) and a weak positive effect on $1{-}D$ (0.001, $p = 0.022$). No climate or vegetation predictor is significant for S, H, or $1/D$. Precipitation has no significant effect on any index.

Random effects stability. The Group SD, year SD, and ICC values change negligibly between Models 1 and 3, confirming that the random effect structure is not sensitive to the inclusion of climate predictors. The dominant source of variance remains between-route identity in all models.

Ecological interpretation. Together, Models 1–3 indicate that long-term trends in North American breeding bird biodiversity are driven by processes other than broad-scale climate variation and vegetation productivity as captured by these indices. The most likely candidates include land-use change (agricultural intensification, urbanisation, and forest management), long-range shifts in migratory connectivity, and species-specific population dynamics. The sharp decline in N and the coincident increase in evenness are consistent with documented collapses of numerically dominant species – particularly abundant granivores – which compress the upper tail of the abundance distribution and raise diversity indices mechanically, even as total bird numbers fall.

Conclusions. Analysis of 24 years of BBS data using linear mixed-effects models reveals consistent, statistically significant trends in local breeding bird biodiversity across North America. Mean local species richness, Shannon diversity, and evenness all increased moderately between 1984 and 2007, while total abundance declined. These trends are characterised by substantial spatial heterogeneity (large random slope variances), and routes with higher baseline diversity tend to experience more adverse trends (negative random intercept–slope covariance).

Climate variables (temperature and precipitation) and vegetation greenness (NDVI) are not the primary drivers of these trends: adding them to the models causes no meaningful reduction in the year coefficient for any diversity index. Temperature is associated with interannual variation in total abundance, but this association does not account for the directional decline. The observed trends most likely reflect land-use and habitat changes and the collapse of specific dominant species, rather than broad climatic forcing over this period.

From a conservation standpoint, the sustained decline in total abundance despite increasing evenness is a warning signal. Historically common species – whose abundance once suppressed diversity indices – appear to be declining, producing a paradox of rising evenness within declining communities. Conservation strategies should therefore focus not only on gamma-scale metrics (how many species survive somewhere) but on protecting locally abundant, functionally important populations across the full range of BBS routes.

Methodologically, LMMs provide a powerful and principled framework for long-term biodiversity monitoring data. Compared with location-by-location regression, LMMs (i) produce more reliable site-specific trend estimates through partial pooling; (ii) test for global trends within a single model, avoiding the multiple-comparison burden of aggregating hundreds of individual tests; (iii) formally decompose variance into alpha-level (fixed effects) and beta-level (random effects) components; and (iv) appropriately handle the clustered, repeated-measures structure of monitoring data. The explicit linkage between LMM components and the Whittaker alpha/beta framework makes LMMs a natural analytical language for community ecologists working with spatially replicated time series.

Анотація. Дані довгострокового моніторингу біорізноманіття потребують аналітичних моделей, здатних одночасно відображати тенденції в масштабах континенту та місцеві варіації. Ми застосували лінійні моделі змішаних ефектів (LMM) до даних Північноамериканського обстеження гніздуючих птахів (BBS), що охоплюють 440 маршрутів обстеження та 24 роки (1984–2007), щоб оцінити часові тенденції у шести індексах біорізноманіття – видовій різноманітності (S), загальній чисельності (N), ентропії Шеннона (H) та індексах на основі Сімпсона (D, 1−D, 1/D) – та оцінити, чи можуть клімат (температура, опади) та рослинність (NDVI) пояснити спостережувані тенденції. Фіксовані ефекти в LMM оцінюють тенденції середнього місцевого (альфа) різноманіття, тоді як випадкові ефекти кількісно визначають гетерогенність між локаціями (бета-різноманіття). Усі індекси біорізноманіття показали статистично значущі спрямовані тенденції протягом періоду дослідження. Видове багатство, ентропія Шеннона та індекси, пов'язані з рівномірністю, помірно зростали, тоді як загальна чисельність зменшувалася. Коефіцієнти внутрішньокласової кореляції (ICC = 0,75–0,96) підтвердили, що ідентичність локації пояснювала домінуючу частку варіації в усіх індексах. Кліматичні фактори та рослинність пояснювали незначну частку часових тенденцій: додавання до моделей температури, кількості опадів та індексу NDVI не призвело до істотного зниження коефіцієнта року для жодного індексу, за винятком чисельності. Лінійні змішані моделі (LMM) мають суттєві переваги перед регресією для окремих локацій, зокрема часткове об'єднання інформації з різних ділянок, формальний розклад дисперсії між рівнями альфа та бета, а також достовірні висновки в умовах кластерної структури даних моніторингу.

Ключові слова: Обстеження гніздуючих птахів; моніторинг біорізноманіття; лінійні змішані моделі; альфа-різноманіття; бета-різноманіття; видове багатство; біотична гомогенізація; Північна Америка; довгострокові тенденції; кліматичні ефекти.

REFERENCES

1. Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature,* 486(7401), 59–67. https://doi.org/10.1038/nature11148
2. Harris, I., Osborn, T. J., Jones, P., & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data,* 7(1), 109. https://doi.org/10.1038/s41597-020-0453-3
3. Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., … & Inger, R. (2018). A brief introduction to mixed effects models and their application in evolutionary biology. *PeerJ,* 6, e4794. https://doi.org/10.7717/peerj.4794
4. Pardieck, K. L., Ziolkowski Jr., D. J., Lutmerding, M., Aponte, V., & Hudson, M.-A. R. (2020). North American Breeding Bird Survey Dataset 1966–2019 (ver. 2019.0). U.S. Geological Survey data release. https://doi.org/10.5066/P9J6QUF6
5. Sauer, J. R., Niven, D. K., Hines, J. E., Ziolkowski, D. J., Pardieck, K. L., Fallon, J. E., & Link, W. A. (2017). The North American Breeding Bird Survey, results and analysis 1966–2015. Version 2.07.2017. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland.
6. Seabold, S., & Perktold, J. (2010). Statsmodels: Econometric and statistical modeling with Python. *Proceedings of the 9th Python in Science Conference* (SciPy 2010), 57–61.
7. Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs,* 30(3), 279–338. https://doi.org/10.2307/1943563