

Temporal species stability underpins the link between biodiversity and human health

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Abstract

Biodiversity is known to impact human health, but the complex relationships between species diversity and health outcomes is poorly understood. Measuring the temporal dissimilarity in species composition can be leveraged to understand the stability of biodiversity and corresponding effects on human health, such as life expectancy at birth, and cause-specific mortality rates. We collected nearly 400 million bird observations from 2010 to 2019 at county level in the US, clustered each county into specific pattern groups by biodiversity characteristics, and performed multivariable linear regressions with human health indicators. Our analyses showed that reduced species replacement (regression coefficient -2.26, 95% confidence interval (CI) -3.06 to -1.47) and less variation in nested species loss or gain (regression coefficient -1.86, 95%CI -2.56, -1.16) were associated with increased life expectancy. Human communities exposed to more stable regional species composition demonstrated a longer average life expectancy, decreased mortality rates from high-burden diseases (e.g., neoplasms, respiratory system, and cardiovascular diseases), and a reduced age-specific mortality risk. The results were adjusted for other influential factors and accounted for the regional species richness. Our study provides epidemiological evidence on the importance of biodiversity stability regarding human health, highlighting the pressing need to preserve and enhance biodiversity stability. It offers fresh perspectives on the global biodiversity crisis and emphasizes the potential impact on human health.

Key words: Avian diversity, Ecosystem stability, Environmental factor, Epidemiology, Health disparity, One health

39 **1. Introduction**

40 Since the 1970s, drastic human-induced environmental change has resulted in the loss of ecosystem functions and services
41 from the global to local scales, which has reciprocally affected all aspects of human living (Brondízio et al., 2021; Díaz et al.,
42 2019). The One Health thesis posits that the health of ecosystems and the overall environment form the cornerstone of human
43 health (SCBD, 2017; Zinsstag et al., 2015). There is a general consensus that ecosystems of higher resilience or stability are
44 beneficial for human health, as they provide consistent and sustainable ecosystem services essential for survival and well-
45 being. Resilient ecosystems are better able to adapt to environmental changes and recover from disturbances, thereby reducing
46 the risk of ecosystem degradation that can lead to health challenges (Reid et al., 2005). However, the pathways of these
47 ecosystem–human health interactions are complex and have developed gradually. The contributions of ecosystem’s
48 biodiversity, particularly the variation of living organisms at the species level, to human health represent one of the most
49 important aspects of this interaction (IPBES, 2021; Marselle et al., 2021). A growing body of evidence reports the positive
50 effects of biodiversity, often measured by species richness, on mental (e.g., lower prevalence of depression, anxiety, and stress)
51 (Cox et al., 2017; Methorst et al., 2021), and, more recently, on physical health of local residential human population (e.g.,
52 reduced mortality rates from cardiovascular diseases and cancer) (Chen et al., 2023). However, the traditional metric of
53 biodiversity, species richness (i.e., count of species numbers in a given locality), might not adequately indicate the relevant
54 function and service of ecosystems (Mori et al., 2013). For example, while two sites might have the same number of species,
55 their species composition (i.e., the identity of the species presenting in a community) can be different, exhibiting substantially
56 different functional traits, which correspond to diverse sets of ecosystem services (Graham and Fine, 2008). There is evidence
57 that different functional traits of various species (such as color, sound, smell, texture, and behavior) can elicit different types
58 of well-being in humans (including physical, emotional, cognitive, social, spiritual, and overall well-being) (Fisher et al.,
59 2023). Moreover, a single species can support multiple traits, leading to diverse feedback across different aspects, illustrating
60 the complexity of how species composition stability influences health experiences (Fisher et al., 2023). For example, the
61 sounds and colors of different bird species may deliver varying health responses. Consequently, many studies that highlight
62 strong biodiversity–human health relationships are often unable to elucidate the mechanisms behind these observed patterns.

63
64 The regional average species richness, referred to as alpha diversity, is a conventional metric in ecological investigations,
65 used to illustrate the spatial distribution patterns of the biodiversity (Whittaker, 1972). Meanwhile, beta diversity has become
66 increasingly prominent in landscape- and global-scale biodiversity studies, as it depicts temporal dissimilarities in species
67 composition of a specific region (Magurran et al., 2019). Shifts in species composition over time can result from both natural
68 and human-induced factors that alter pivotal ecosystem characteristics (Magurran et al., 2010). These factors include
69 environmental stressors such as water, temperature, availability of food resources, and variations in habitat size and quality,

70 all of which are crucial elements of ecosystem stability (Mori et al., 2013). Simply put, the fewer shifts in species composition
71 within a given locality over time (i.e., temporal beta diversity), the more stable the ecosystem. Widely used beta diversity
72 metrics, e.g., the Sørensen dissimilarity index, can be further partitioned into turnover and nestedness components (Baselga,
73 2010). Temporal species turnover refers to species dissimilarity resulting from the replacement of species over time, whereas
74 pronounced temporal nestedness indicates that species dissimilarity stems from the gain or loss of species over time (Baselga,
75 2012; Baselga et al., 2015). Species turnover and nestedness that diverge significantly from a stochastic pattern can signify
76 markedly different processes related to ecosystem stability. Turnover-related patterns are often linked to shifts in key
77 environmental factors over time or across sites, such as climate change or land cover change (Da Silva et al., 2018; Hu et al.,
78 2020; Li et al., 2022). Meanwhile, nestedness-related patterns are often associated with increase or decrease in resources or
79 environmental stress within the ecosystem (Angeler, 2013; Jacquemyn et al., 2007; Stuart et al., 2017).

80
81 Birds have been recognized as suitable biodiversity indicators in regional studies, as they reflect variations in biodiversity
82 across time and space (Chen et al., 2023; Methorst et al., 2021). Birds are abundant, mobile, and highly responsive to
83 environmental and ecological changes, marking their presence and/or absence a reliable indicator of ecosystem changes within
84 their habitats. In this study, we aim to use longitudinal data to assess and illustrate the stability of biodiversity within a local
85 ecosystem, while also reveal its relationship with human health. We hypothesize that unstable temporal species composition
86 is associated with adverse physical health outcomes such as reduced life expectancy at birth, higher age-specific mortality
87 risks, and higher cause-specific mortality rates. Our hypotheses are based on the following aspects: first, ecosystem services
88 may act as potential mediators indirectly linking biodiversity stability to human health. Biodiversity contributes to the delivery
89 of ecosystem services, which include provisioning services such as clean air, safe drinking water, food security, regulating
90 services, and climate stability (Reid et al., 2005). Changes in biodiversity may act as an indicator for the provision of these
91 services, which, in turn, could impact human health. Second, there may be a potential shared factor between biodiversity
92 stability and health, or a direct association between them (Cardinale et al., 2012; Pecl et al., 2017). While most related studies
93 are based on theoretical literature, our study represents the first analytical attempt in this area. Additionally, we hypothesize
94 that the magnitude of this association is modulated by the species richness (i.e., alpha diversity) which represents the
95 fundamental characteristic of biodiversity. Using the eBird database (Sullivan et al., 2009), one of the world's most extensive
96 citizen science biodiversity databases, and health data from the Institute for Health Metrics and Evaluation (IHME), we
97 examined the county-level variation of the species composition from 2010 to 2019 across the United States (US). We then
98 assessed its association with human health by incorporating this temporal variation into a multivariable regression model,
99 after adjusting for other potential influential factors and accounting for rarefied regional species richness. Latent class analysis
100 was used to measure the real-world biodiversity patterns by categorizing each county into a distinctive cluster based on both

101 regional species richness and temporal species composition dissimilarities. Finally, we explored and discussed the regional
102 associations between these derived geographical clusters and health indicators of the local residents.

103 **2. Method**

104 **2.1 Settings**

105 This study was carried out across the US, from 2010 to 2019, at the county (or county equivalent (e.g., District of Columbia))
106 level. The United States has diverse climate types and, as a continental-scale country, spans a wide geographical range with
107 oceans on both coasts. Meanwhile, as a developed nation, it offers comparable healthcare coverage across the country, along
108 with comprehensive socioeconomic data, demographic characteristics, and medical records. Lastly, the eBirds database
109 provides extensive records at the county level, making it a valuable resource for analysis. These factors collectively make the
110 US an ideal location for conducting this environmental epidemiology research. Data was collected from multiple perspectives,
111 including 1) bird diversity indicators (species composition dissimilarities as explanatory variables assessing the biodiversity
112 stability, and rarefied species richness reflecting regional difference), 2) human health statistics as response variables. This
113 study used the general health indications such as life expectancy and cause-specific mortality rates, rather than disease
114 diagnoses, to control for possible variations in disease detection and recording standards across the US. Certain health
115 measurements can be influenced by detection abilities and survival duration, for example, a higher rate of a particular disease
116 could potentially be a result of more advanced diagnostic methods or treatments increasing the survival periods. However,
117 life expectancy and cause-specific mortality data are less problematic for large-scale research across various geographical
118 locations and offer a less biased measurement of overall health. In this study, we also made adjustments for potential
119 confounding effects, based on a carefully compiled list of covariates, encompassing population structure, socio-demographics,
120 healthcare service, residential environment, as well as geographical and climatic characteristics.

122 **2.2 Biodiversity indicators**

123 Bird diversity data was sourced from the eBird database (<https://ebird.org/home>, data downloaded on 28th July, 2022), a citizen
124 science platform managed by the Cornell Lab of Ornithology. It is one of the world's largest biodiversity-related projects, with
125 millions of bird sightings contributed each year around the world. The database provides an ample amount of data on bird
126 species distribution and abundance, making it a valuable resource for scientific research and conservation initiatives. The data
127 contained within the eBird database is a collection of numerous observation events, accumulated by an extensive community
128 of users. Each of these observation events is singly uploaded and documented by an observer (or group), including observed
129 bird species, quantities, time, date of observation, the locale of the sighting, and the duration of birdwatching activity (Sullivan
130 et al., 2009). To uphold data integrity, we retained years with a data completeness rate surpassing 90%, and also addressed
131 potential instances of incomplete observations and systematic error. We reviewed all the records leading up to the date of data

download (the database was updated until the year 2020), and henceforth, confined our research timeline from the year 2010 through to 2019.

2.2.1 Rarefied species richness of birds (alpha diversity)

After compiling a decade's worth of avian data, we tallied a total of 24,912,327 identified observation events in 3140 counties, encompassing over 396 million observations and 1,843 bird species. Simultaneously, in order to mitigate bias caused by uneven regional observation intensity, counties with fewer than 150 observation events were defined as having insufficient observations within the integrated database (Chen et al., 2023). After excluding counties with inadequate observations, we employed a rarefaction technique to ensure comparable levels of bird species richness across each county (Heck et al., 1975; McMurdie and Holmes, 2014). We undertook repetitive random sampling of the entire bird population in each county, with the sample size (3,737) based on the county with the minimal bird abundance. This approach aimed to achieve optimal rarefaction accuracy under the condition of maximum samples (Zou et al., 2023). This particular process was done using R (version 4.3.1) package “vegan” with its internal function “rarefy” (Oksanen et al., 2015). After the whole process, in total, data of rarefied species richness of birds in 2,985 counties were analyzed for this study period.

2.2.2 Species composition dissimilarities (beta diversity)

To further assess the ecosystem stability, a multiple-site proxy based on Sørensen dissimilarity index was employed through a method proposed by Baselga to measure the temporal shifts in species composition (β_{SOR}), which was independent from the alpha diversity (rarefied regional species richness) (Baselga, 2010; Sørensen et al., 1948). To delve deeper into the specific patterns of species composition differences, Sørensen-based dissimilarity was partitioned into two mutually independent components, denoted as Turnover (Simpson-based dissimilarity β_{SIM}) and Nestedness (Nestedness-resultant dissimilarity β_{NES}) (Baselga, 2010, 2007; Lennon et al., 2001; Simpson, 1943). The former referred to the change in faunal composition caused by species replacement, i.e., the temporal trade-off between extinction and immigration, whereas the latter evaluated the portion of compositional change due to nested species gain or loss (Baselga et al., 2015; Habel et al., 2016). In order to calculate these dissimilarities, we constructed a binary matrix for each of the 2985 counties, each matrix cataloguing all 1843 bird species along with a yearly record of whether they were observed (presence/absence), thereby accounting for the temporal fluctuation in the bird species. The detailed mathematical formulas and methodologies were supplied in Note S1. The range of values of these three dissimilarities was between 0 and 1, with lower values indicating less variation in species composition caused by the corresponding factor and reflecting higher ecological stability. All indices were computed using R, using the package “betapart” with its internal function “beta.multi” (Baselga and Orme, 2012).

Box 1. The key definitions of biodiversity terms**Alpha diversity:** The regional average species richness

A measurement of alpha diversity:

Rarefied species richness: Estimated regional total species richness**Beta diversity:** Species composition shifts in a given locality over time

Measurements of beta diversity:

Simpson-based dissimilarity (β_{SIM}): Change in species composition caused by species replacement, ranging from 0 to 1, with larger values being more unstable.**Nestedness-resultant dissimilarity (β_{NES}):** Compositional change due to nested species gain or loss, ranging from 0 to 1, with larger values being more unstable.**Sørensen-based dissimilarity (β_{SOR}):** Total temporal species compositional differences, ranging from 0 to 1, with larger values being more unstable.

(Sørensen-based dissimilarity = Simpson-based dissimilarity + Nestedness-resultant dissimilarity)

164 **2.3 Human health statistics**

165 Human health data, including life expectancy at birth, the change in life expectancy, cause-specific mortality rate, and age-
 166 specific mortality risk, was obtained from the Institute for Health Metrics and Evaluation (IHME). In order to capture the
 167 county-level life expectancy, to the database from IHME considered population data from the US National Centre for Health
 168 Statistics and death registration data from the US National Vital Statistics System (GBD US Health Disparities Collaborators,
 169 2022). With the adjustments on mortality rates, an abridged life table at the county (or county equivalent) level was constructed
 170 for life expectancy at all ages (GBD US Health Disparities Collaborators, 2022). In this dataset, we used the life expectancy
 171 at birth in 2019 as well as the change of that from 2010 to 2019 for the corresponding study period. The latest Global Burden
 172 of Disease Study (GBD 2019), published within the IHME and the Lancet, featured risk summaries relating to diseases,
 173 injuries, and impairments derived from a total of 204 countries and territories worldwide (Vos et al., 2020). In this repository,
 174 we amassed county-level statistics from the US for the year 2019, which featured age-standardized mortality rates according
 175 to 19 specific causes from non-communicable diseases, infectious ailments, and injuries (Dwyer-Lindgren et al., 2023;
 176 Institute for Health Metrics and Evaluation (IHME), 2023). Additionally, we concurrently obtained the age-specific mortality
 177 risks in the most recent period (2014), where the ages were divided into the five categorical groups, 0-5, 5-25, 25-45, 45-65,
 178 and 65-85 (Dwyer-Lindgren et al., 2017; Institute for Health Metrics and Evaluation (IHME), 2017). Since data in 2019 was
 179 not available for age-specific mortality risks, relevant results only served as additional references.

181 **2.4 Other covariates**

We paid great effort into considering the inclusion of covariates, ensuring comprehensive coverage of variables potentially associated with human health, based on the evidence from relevant literature (Eide and Showalter, 2011; Gallet and Doucouliagos, 2017; Marmot, 2005; Pickett and Wilkinson, 2015), as well as our previous research. County-level statistics at baseline in 2010 (or the nearest year for which data are available) for consideration in statistical adjustments were collected from the US Census Bureau and National Oceanic and Atmospheric Administration, including population information (i.e., population size, gender, ethnicity, and age), socio-demographics (i.e., education, household income, unemployment and poverty rate), healthcare (i.e., health insurance coverage and physicians as a proportion population), residential environment (i.e., Rural-Urban Continuum Area Code) and geographic and climatic characteristics (i.e., total area, latitude, longitude, annual average temperature, and annual precipitation).

2.5 Statistical analysis

Over the study period, we gathered dissimilarities denoting temporal variation in bird species composition and considered rarefied species richness as the spatial measurement. Data pertaining to life expectancy at birth was collected as the primary outcome variable. In addition, from longitudinal perspective, the change in life expectancy from 2010 to 2019 was enrolled as an additional outcome. Cause-specific mortality rates and age-specific mortality risks were employed as secondary outcome variables.

Descriptive statistics on studied variables were reported first, including the biodiversity indicators, county-level statistics on covariates, and human health data. The research design of the regression modelling was divided into two stages. The first stage involved exploring the preliminary associations between species composition differences and human life expectancy to establish a foundation for subsequent analyses in this paper. In this stage, univariable linear regression analyses were initially undertaken to assess the relationship between each studied variable and life expectancy as well as the change in life expectancy. Then, multivariable linear analyses were employed to assess the association between species compositional dissimilarities (β_{SIM} and β_{NES}) and health statistics with the consideration of rarefied species richness and adjustments for potential influential factors. However, the overall Sørensen-based dissimilarity was excluded from the model due to the violation of multicollinearity among the beta dissimilarities ($\beta_{SOR} = \beta_{SIM} + \beta_{NES}$).

In the second stage, latent class analysis was conducted by integrating the significant biodiversity indicators in multivariable model from the previous stage to evaluate the overall diversity pattern for each region (Schreiber, 2017). To further classify the samples into potential clusters with latent characteristics, each county was only allocated to one cluster. The clustering process was programmed by the Latent GOLD (version 5.0). In the current study, we reported information criterion values

213 for each model with a different number of clusters, including Log-likelihood statistics (LL), the percentage reduction of LL
214 from the null hypothesis (i.e., model with one cluster only), Bayesian Information Criterion (BIC) and Consistent Akaike's
215 Information Criterion (CAIC). We also imposed a constraint specifying that the smallest cluster size must not fall below 10%
216 in order to maintain sufficient sample size of each cluster. The optimal model was determined by selecting the one with best
217 explanation of the data, subject to the condition of having an adequate sample size. Subsequently, counties were assigned to
218 a specific cluster based on their posterior probabilities within each cluster. Eventually, we incorporated the clustering result
219 into multivariable linear regression models as a categorical variable for investigating the association between biodiversity
220 patterns and human health with the adjustments for potential confounding factors. Human health indicators were separately
221 employed as outcome variables, including life expectancy at birth, change in life expectancy, cause-specific mortality rates
222 (per 100,000 population), and age-specific mortality risks (risk of death in %). We reported regression coefficients and R^2 in
223 models related to life expectancy. The regression coefficient quantifies the effect size of individual factors per unit change in
224 health measurements, while the R^2 reflects the proportion of the response variable explained by predictor variables.

225
226 Finally, through the method of variance partitioning analysis (Hoffman and Schadt, 2016), we listed all studied parameters
227 via standardized regression coefficients to explore the proportion of each biodiversity parameter contributing to the model
228 within each cluster. This, in turn, provided quantitative measurement of their impact on the life expectancy under various
229 diversity patterns.

230
231 During the initial stage, we employed a relatively standard threshold (a p value < 0.05 , two tailed) with life expectancy as the
232 response variable, thereby drawing preliminary inferences. In the second stage pertaining to mortality-related analysis, we
233 instituted a more stringent threshold (a p value < 0.001). This strategy amplified the credibility of the potential inferences and
234 aimed for conservative results with low level of false positive findings. When conducting sensitivity analysis, we initially set
235 a gradient cut-off value by identifying insufficient observations as less than 50, 200, 300, 500, 1500 events, and then repeated
236 the aforementioned rarefaction process. Then, we conducted the same process of statistical analyses against different outcome
237 variables. This is a "trade-off" process that aims to accommodate as many samples as possible while ensuring that the results
238 are robust with highest possible statistical power (largest sample size). Unless otherwise specified, all analyses were carried
239 out using R (version 4.3.1).

241 **3. Results**

242 The county-level descriptive statistics of biodiversity indicators, population information, socio-demographics, healthcare
243 service, residential environment, and geographic and climatic characteristics in the US are presented in Table 1. The mean

244 value of Sørensen-based dissimilarity was 0.534, with a standard deviation (SD) of 0.118. When examining its components,
245 the Simpson-based dissimilarity (mean 0.347, SD 0.090) was approximately twice that of the Nestedness-resultant
246 dissimilarity (mean 0.187, SD 0.084) on average. The results suggested that, during the study period, the principal cause of
247 species composition variation (β_{SOR}) in the US was primarily explained by species replacement (β_{SIM}) compared to nested
248 species loss or gain (β_{NES}). The global patterns of these biodiversity indicators across the US are shown in Figure S1.

249
250 The average life expectancy at birth was 77.52 years with a SD of 2.54. Among all causes of death, the top six were
251 cardiovascular diseases, neoplasms, chronic respiratory diseases, neurological disorders, diabetes and kidney diseases, and
252 digestive diseases (Table S1). Age-stratified mortality risks are shown in Table S2. From a longitudinal perspective over the
253 study period, the average life expectancy has remained relatively stable.

254
255 The results of the initial univariable linear regression were presented in Table 2. However, dissimilarities in species
256 composition were negatively associated with life expectancy. For every increase of 0.1 in the Sørensen-based dissimilarity
257 (unstable species composition), the average life expectancy was anticipated to decline by 0.68 years. The proportion of
258 variance explained by Sørensen-based dissimilarity (R^2 , 10%) exceeded a list of variables including, rarefied species richness
259 of birds, healthcare service and residential environment, demonstrating its importance (Table 2). In the multivariable analyses,
260 after adjusting for other influential factors and rarefied species richness of birds, the less Simpson-based (less variation in
261 species composition caused by replacement) (regression coefficient -2.262, 95%CI -3.057 to -1.467) and Nestedness-resultant
262 dissimilarities (less compositional change due to species gain or loss) (regression coefficient -1.856, 95%CI -2.557 to -1.156)
263 were significantly associated with the longer life expectancy. With the same statistical approach, similar results were obtained
264 with a significant association between a more stable species composition (β_{SOR}) and an increase in change in life expectancy
265 from 2010 to 2019 (Table S3).

266
267 Simpson-based dissimilarity, Nestedness-resultant dissimilarity and Rarefied species richness of birds were included for latent
268 class analysis, and the result showed that the four-cluster model, given a sufficient sample size in each derived cluster (i.e. >
269 10% of the total number of samples), reached the optimum explanatory efficacy with the lowest CAIC and BIC (Table S5).
270 Each studied county was allocated into one of the four distinctive clusters: Cluster 1 (n=996 (33.37%), a scarcity of richness
271 and a highly unstable structure due to species replacement), Cluster 2 (n=919 (30.79%), a transitional pattern with moderate
272 richness), Cluster 3 (n=536 (17.95%), a diverse cluster with relative stable species composition), and Cluster 4 (n=534
273 (17.89%), relatively low species nestedness) (Table 3). The geographical distribution of the latent class analysis-derived
274 biodiversity clusters and life expectancy are shown in Figure 1. For South Atlantic and East South-Central areas, the

275 distribution of Clusters 1 and 2 occupied a dominant proportion, while the corresponding life expectancy was relatively low;
276 whereas in East north central, Northeast and West areas, higher life expectancy appeared with Clusters 3 and 4.
277

278 Significant disparities in life expectancy were seen among populations residing in different clustering regions: Compared to
279 other clusters, population living in Cluster 1 exhibited a significantly reduced life expectancy after adjustments for other
280 influential factors (Table 4). On the other hand, population in Cluster 4 was associated with the longest life expectancy, and
281 on average it was 0.558 years longer than that in Cluster 1. Apart from the growth observed in Cluster 4 compared to Cluster
282 1, there were no significant differences observed in terms of changes in life expectancy across the different diversity patterns
283 (Table S4).
284

285 Considerable health disparities, regarding the cause-specific mortality rates, were found between Cluster 1 and other clusters
286 (Figure 2). Population residing in Clusters 3 and 4, featured with higher avian species richness and stable diversity structures,
287 exhibited distinctly lower mortality rates of many diseases including cardiovascular diseases, neoplasms, chronic respiratory
288 diseases, and respiratory infections and tuberculosis, compared to those living in cluster 1 (featured with lower species
289 richness and unstable temporal composition).
290

291 Regarding age-specific mortality risks, in general, populations residing in Clusters 3 and 4 exhibited significantly lower
292 mortality risks across all age groups compared to those residing in Cluster 1 (Figure S2). Only in the elderly age group (65-
293 85 years), population residing in cluster 2 demonstrated significantly lower mortality risks than that residing in Cluster 1.
294 Finally, we also found that with the progression of age groups, the association between each clustering group and the risk of
295 mortality exhibited an increasingly disparate result, given that as age advanced, the natural mortality risks increased.
296

297 In the context of variance partitioning analysis, the relative effect proportion of counties in different clusters showed that in
298 regions with higher species richness, the species richness itself could explain more variation in the life expectancy (Figure 3).
299 However, for all studied counties, the dissimilarity of species composition occupied a larger relative effect on the response of
300 life expectancy, compared to species richness. In other words, the temporal turnover of species, as well as the loss and
301 introduction of species, have a better explanation and higher association with life expectancy than regional species richness
302 in the current samples.
303

304 Sensitivity analyses, according to the different cut-off thresholds (100, 150 (as the reported results), 200, 500 and 1500) on
305 the minimum requirement of adequate observations in each county for study sample inclusion, revealed the robust findings.

306 The omitted counties (n = 154) in the study exhibited poorer life expectancy. Additionally, they had smaller populations, with
307 the vast majority being completely rural areas, which also suggested insufficient observation events as a potential reason for
308 exclusion. Although the exclusion proportion was very small, these counties accounted for only a small fraction of the United
309 States (4.9%) in the study. The summary characteristics of these counties were presented in Table S8.

311 **4. Discussion**

312 **4.1 High biodiversity stability benefits human health**

313 Our results indicate that the stability of species' temporal composition was associated with several indices of human physical
314 health. After accounting for species richness and adjusting for other common influential factors, the Simpson-based and
315 Nestedness-resultant dissimilarities demonstrated a significant negative association between the stability of species temporal
316 composition and life expectancy. This implies that, in terms of temporal dimension, there existed a relationship between the
317 instability of ecosystems (i.e., the introduction of new species, the loss of existing ones, and the substitution of species) and
318 the declines in human health. Latent class analysis was employed to reveal the natural geographic patterns of biodiversity
319 distribution in the US and assess their associations with health outcomes. This approach reflected real-world exposure
320 scenarios and cumulative effects from various aspect of biodiversity features. This highlighted hotspot of biodiversity
321 represented areas in need of conservation efforts or regions showing significant changes in species composition on real-world
322 map. By capturing the diversity patterns of the real-world, it allowed us better to observe, analyze and summarize the
323 relationship between health and biodiversity from different perspectives (i.e., different clustering results), providing a method
324 closely aligned with ecological principles. When simultaneously considering the aspects of richness and stability, all regions
325 were categorized into four clusters with distinct characteristics. Significant associations were found between the clusters
326 characterized by higher species richness and more stable species composition and various positive health outcomes. These
327 outcomes included an extended life expectancy, reduced mortality rates for specific causes, and diminished overall mortality
328 risk across age groups. Notably, these discrepancies were particularly conspicuous among the most concerned burden of
329 human health problems, such as cardiovascular diseases, neoplasms, chronic respiratory diseases, diabetes and kidney diseases,
330 and respiratory infections. Additionally, it appeared that the correlational effects arising from this stability were even greater
331 than the inherent species richness. After all parameters were scaled to a comparable level after data standardization, within
332 the context of variance partitioning analysis, the influence exerted by the stability of species composition on human health far
333 surpasses the explanation provided by species richness (Figure 3). Especially in regions where bird diversity was relatively
334 deficient, it was the stability of diversity composition, surpassing richness itself, that predominantly explained the positive
335 outcome of human life expectancy. While our methodology cannot establish a causal relationship, it has provided robust
336 statistical evidence of associations between biodiversity stability and human health, thereby emphasizing the tangible impact

of stability of biodiversity in ecosystem on human health.

These results are significant at a time where ecosystem change is rapid and widespread. As noted in the Millennium Ecosystem Assessment, there is established but incomplete evidence to suggest that the stability of ecosystem is undergoing certain changes, which can have significant implications for human health (Ives and Carpenter, 2007; Martinez-Juarez et al., 2015; Pennekamp et al., 2018; Reid et al., 2005). To the best of our knowledge, the majority of research inquiries revolve around conducting association studies on specific indicators within the realms of ecosystems and biodiversity. Avian and botanical diversity, greenness, verdant landscapes, natural vegetation coverage, and atmospheric health are all common indicators potentially interacted with human physical health and mental well-being. In the majority of studies in this regard have consistently underscored a positive association (Aerts et al., 2018; Chen et al., 2023; Fuller et al., 2007; Luck et al., 2011; Methorst et al., 2021; Wheeler et al., 2015), however, some have yielded different conclusions (Cox et al., 2017; Dallimer et al., 2012; Fisher et al., 2021). For instance, a small-area study conducted in entire Spain on the association of air pollution and greenness with mortality and life expectancy from 2009 to 2013 found that increased air pollutants were significantly associated with the decrement in life expectancy and a surge in mortality rate (de Keijzer et al., 2017). The greenness was observed to be related to the outcome variables only in regions with relatively poor socio-economic status. Regrettably, there exists a noticeable dearth of studies that take species composition difference or stability as a focal point. Our current study further suggests that the temporal stability in species composition was associated with the enhanced human health, considering both common socio-demographic determinants and the richness of the species. Additionally, biodiversity patterns with greater stability and species richness could potentially contribute to better human health.

4.2 Stable Biodiversity Ecosystem Functioning and Human Physical Health

Higher temporal Sørensen-based dissimilarity, indicative of beta species diversity, suggests increased ecosystem instability. Our study also reveals that counties with higher beta diversity exhibit notably lower species richness (as shown in cluster 2 of Table 3). This finding elucidates a mechanism supporting the positive link between biodiversity and physical health outcomes unveiled in our previous work (Chen et al., 2023). Biodiversity is widely recognized for its stabilizing effects on ecosystem processes, functions and services, despite the variability in the stability of individual species (Balvanera et al., 2006; Loreau and De Mazancourt, 2013). Enhanced biodiversity may bolster ecosystem stability through the increasing of ecological interactions, augmentation of interspecific complementarity, efficient utilization of limited resources, expanded nutrient reserves (Tilman et al., 2014; Valiente-Banuet et al., 2015). Such stabilizing effect is especially critical in light of severe environmental crisis, like the rapid loss of primary habitats and global climate change (Sandifer and Sutton-Grier, 2014). Our findings indicate that such stability stemming from biodiversity in ecosystem functioning yields cumulative

368 advantages for human physical health, as evidenced by increased life expectancy. On the other hand, ample empirical data
369 have shown that the accelerated degradation of ecosystems, such as habitat loss, trophic collapse, and environment pollution,
370 will result in the shift and loss of species within the ecosystem (Dobson et al., 2006). The intricate link between biodiversity
371 and ecosystem functioning forms the foundation for the beneficial impacts of biodiversity on human health. The decline in
372 ecosystem services can mirror and contribute to the reduced stability of species composition in a region, which ultimately
373 leads to adverse effects on human health (Myers et al., 2013). This holistic perspective linking biodiversity, ecosystem
374 functioning, and human health aligns with the One Health concept (SCBD, 2017). Furthermore, it highlights the synergistic
375 effects of achieving Sustainable Development Goals that pertain to the conservation of nature and the enhancement of human
376 health. We can infer from our study that the stability of bird species composition significantly correlates with life expectancy,
377 reflecting the interconnectedness of ecosystems and human health. Our findings underscore the importance of not just
378 biodiversity, but also the stability of species composition within an ecosystem. Rather than solely focusing on species richness,
379 i.e., the number of different species present in an area, our study suggests that the stability of species composition might be a
380 more nuanced measure of an ecosystem's health and vitality. This stability, representing the balance and consistency of species
381 distribution over time, could possibly explain the human health. Hence, it's crucial that we broaden our perspectives on
382 biodiversity and incorporate both species richness and stability of species composition into our biodiversity evaluations for
383 more comprehensive and accurate insights.

384 **4.3 Strength and limitations**

386 This study used county-level data reported at smallest available administrative unities with broad coverage. In health
387 epidemiology, this type of analysis is referred to as an 'ecological study', which is not to be confused with the way that this
388 term would be used in the disciplines of environmental science and ecology (where an ecological study would be undertaken
389 to understand complex interactions within environmental systems). It leveraged comprehensive data on demographics,
390 socioeconomic conditions, healthcare services, residential environmental statistics, and climatic and geographical features at
391 the county level, as recorded by the US federal agencies. This allowed for a detailed adjustment of confounding variables in
392 the statistical examinations. This research employed a partitioning dissimilarity representation of species composition based
393 on Baselga algorithm. In comparison to other partitioning such as additive algorithm, multiplicative algorithm, and
394 dissimilarity based on Podani & Schmera (POD) method, Baselga approach derived a temporal multisite index that is
395 independent of species richness (Anderson et al., 2011; Chao et al., 2012; Crist and Veech, 2006; Podani and Schmera, 2011;
396 Shengbin et al., 2010; Si et al., 2017). We analyzed it using the world largest bird observation database over a decade. On this
397 basis, the impact of regional variations in species richness could be considered while investigating the stability of species and
398 human health. However, this study also presents certain limitations. A notable challenge in ecological studies in health

399 epidemiology is the so-called 'ecological fallacy,' whereby associations observed at the group level, such as county-level data,
400 may not accurately represent the true relationships for individuals within those groups. Additionally, typical issues related to
401 ecological studies, such as bias due to population migration, may affect the results. Detailed mechanisms cannot be addressed
402 in this environmental epidemiology setting, and future research is needed to unravel these complexities.

404 **5. Conclusion**

405 This paper emphasizes the importance of considering biodiversity in terms of species composition stability. Our findings
406 suggest that species composition stability is more important than richness in certain contexts, with communities exposed to
407 higher species richness and more stable species composition demonstrating improved health outcomes. This insight prompts
408 us to consider the role biodiversity plays in public health and emphasizes the urgency to maintain and improve the biodiversity
409 stability. The study thereby advocates for a more nuanced examination of biodiversity characteristics, providing new insights
410 into the implications of the global biodiversity crisis and its potential impacts on human health.

412 **Data availability:**

413 Data sets generated during the current study are available from the corresponding authors on reasonable request. The sources
414 of raw data were available within the paper, its additional file 1 (Table S7) and corresponding references.

415
416 **Declaration of competing interest:**

417 The authors declare they have no conflicts of interest related to this work to disclose.

418
419 **Author Contributions:**

420 **Q.X.:** Formal analysis, Data curation, Visualization, and Writing – original draft. **Y.C.:** Conceptualization, Writing – review
421 and editing, Supervision, and Funding acquisition. **L. L.:** Conceptualization, Writing – original draft, Writing – review and
422 editing, Supervision. **B.Q.:** Data curation, and Formal analysis. **P.Z.:** Methodology, and Writing – review and editing. **S.C.:**
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Table 1. County-level descriptive statistics of biodiversity indicators, population information, socio-demographics, healthcare service, residential environment, and geographic and climatic characteristics in the US.

Variables	Number (%), or median (IQR)
Biodiversity	
Sørensen-based dissimilarity	0.53 (0.43, 0.63)
Simpson-based dissimilarity	0.33 (0.28, 0.41)
Nestedness-resultant dissimilarity	0.18 (0.12, 0.24)
Rarefied species richness of birds	150.07 (133.68, 165.8)
Population information	
Population size	27,822 (11,982, 71,404)
Gender, male	49.53% (48.89%, 50.38%)
Ethnicity, white alone	92.83% (81.46%, 96.7%)
Age, years	
0-9	12.51% (11.33%, 13.73%)
10-19	13.54% (12.6%, 14.45%)
20-29	11.31% (9.86%, 13.04%)
30-39	11.58% (10.55%, 12.54%)
40-49	13.64% (12.78%, 14.5%)
50-59	14.56% (13.61%, 15.56%)
60-69	10.85% (9.62%, 12.24%)
70-79	6.51% (5.45%, 7.62%)
80 and over	4.09% (3.27%, 5.04%)
Socio-demographics	
Education level, 25 years and over	
Less than a high school diploma	14.64% (10.77%, 20.31%)
A high school diploma only	57.59% (53.16%, 61.52%)
Completing some college or associate's degree	7.52% (5.99%, 9.09%)
A bachelor's degree or higher	17.44% (13.62%, 23.17%)
Median household income (annual, US dollar)	41,612 (36,508, 48,195)
Unemployment rate, age < 65	9.1% (7.2%, 11.2%)
Poverty rate	15.7% (12.1%, 19.9%)
Healthcare service	
Health insurance coverage, age < 65	81.9% (78%, 85.7%)
Physicians per thousand population	0.82 (0.43, 1.54)
Residential environment (Rural-Urban Continuum Area Code)	
1 (Metro areas, 1 million population or more)	426 (14.27)
2 (Metro areas, 250 thousand to 1 million population)	376 (12.60)
3 (Metro areas, population fewer than 250 thousand)	346 (11.59)
4 (Urban population of 20 thousand or more, adjacent to a metro area)	213 (7.14)
5 (Urban population of 20 thousand or more, not adjacent to a metro area)	92 (3.08)
6 (Urban population of 2,500 to 19,999, adjacent to a metro area)	570 (19.10)
7 (Urban population of 2,500 to 19,999, not adjacent to a metro area)	399 (13.37)
8 (Completely rural or less than 2,500 urban population, adjacent to a metro area)	196 (6.57)
9 (Completely rural or less than 2,500 urban population, not adjacent to a metro area)	367 (12.29)
Geographic and climatic characteristics	
Total Area, square mile	665.12 (457.28, 1009.41)
Longitude	-90.44 (-98.52, -83.43)

Latitude	38.45 (34.73, 41.91)
Average temperature, Fahrenheit scale	54.68 (48.64, 60.73)
Annual precipitation, inches	38.6 (30.12, 44.71)

758 IQR, interquartile range. Based on 2985 studied US counties. Gender (male as reference category), the other category: female.
759 Ethnicity (white alone as reference category), other categories: Black or African American, American Indian and Alaska
760 Native, Asian, Native Hawaiian and Other Pacific Islander, and Others. Residential environment (categorical variable),
761 presented as “count (percentage)”. Other variables (continuous variable), presented as “median (IQR)”.

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Table 2. Regression analyses for the association between composition dissimilarities and life expectancy at birth with and without adjustments for rarefied species richness and other potential confounding factors.

Variables	Univariable analysis		Multivariable analysis	
	Regression coefficient (95% CIs)	R ²	Regression coefficient (95% CIs)	R ²
				0.667
Biodiversity				
Simpson-based dissimilarity	-7.891 (-8.87, -6.913)	0.077	-2.262 (-3.057, -1.467)	
Nestedness-resultant dissimilarity	-4.525 (-5.603, -3.447)	0.022	-1.856 (-2.557, -1.156)	
Sørensen-based dissimilarity	-6.796 (-7.528, -6.064)	0.100	-	
Rarefied species richness of birds	0.022 (0.019, 0.026)	0.059	0.003 (0.001, 0.005)	
Population information				
Population (per million)	1.644 (1.365, 1.923)	0.043	0.555 (0.364, 0.747)	
Male (%)	0.101 (0.06, 0.142)	0.008	0.170 (0.143, 0.198)	
White alone (%)	0.054 (0.048, 0.059)	0.113	0.02 (0.015, 0.024)	
Age ≥ 80 (%)	0.127 (0.068, 0.185)	0.006	0.227 (0.179, 0.275)	
Socio-demographics				
A bachelor's degree or higher (%)	0.186 (0.178, 0.194)	0.410	0.125 (0.114, 0.136)	
Median household income (per thousand US dollars)	0.152 (0.145, 0.158)	0.410	0.058 (0.046, 0.071)	
Unemployment rate, age < 65 (%)	-0.314 (-0.341, -0.287)	0.148	0.016 (-0.006, 0.039)	
Poverty rate (%)	-0.269 (-0.281, -0.258)	0.403	-0.085 (-0.105, -0.065)	
Healthcare				
Health insurance coverage, age < 65 (%)	0.123 (0.108, 0.139)	0.075	-0.066 (-0.081, -0.051)	
Physicians per thousand population	0.417 (0.36, 0.474)	0.065	-0.074 (-0.119, -0.03)	
Residential environment				
Rural-Urban Continuum Area Code		0.077		
1 Metro areas	Reference category		Reference category	
2	-1.024 (-1.364, -0.685)		0.314 (0.093, 0.536)	
3	-1.009 (-1.357, -0.662)		0.581 (0.344, 0.818)	
4	-1.64 (-2.042, -1.237)		0.298 (0.026, 0.571)	
5	-1.383 (-1.935, -0.831)		0.361 (0, 0.722)	
6	-2.284 (-2.592, -1.977)		0.365 (0.131, 0.6)	
7	-1.565 (-1.899, -1.23)		0.382 (0.123, 0.64)	
8	-1.698 (-2.112, -1.283)		0.525 (0.227, 0.824)	
9 Completely rural	-0.857 (-1.199, -0.515)		0.602 (0.312, 0.892)	
Geographic and climatic characteristics				
Total area (per thousand square miles)	0.017 (-0.006, 0.041)	0.001	-0.04 (-0.056, -0.024)	
Longitude	-0.036 (-0.043, -0.029)	0.034	-0.009 (-0.015, -0.004)	
Latitude	0.177 (0.162, 0.193)	0.138	0.066 (0.051, 0.08)	
Average temperature, Fahrenheit scale	-0.126 (-0.137, -0.116)	0.160	-	
Annual precipitation, inches	-0.019 (-0.026, -0.012)	0.009	-0.001 (-0.006, 0.004)	

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CI, confidence intervals. Based on 2985 studied US counties. Average temperature, excluded in multivariable analysis due to multicollinearity with latitude.

770 Table 3. Results of latent class analyses (LCA) including significant biodiversity indicators and indirect influenced
 771 parameter (total studied counties, n= 2985).

Assigned Clusters	Rarefied species of richness of birds	Simpson-based dissimilarity	Nestedness-resultant dissimilarity	Sørensen-based dissimilarity
Cluster 1, n= 996 (33.37%)	132.55	0.45	0.17	0.59
Cluster 2, n= 919 (30.79%)	145.96	0.32	0.27	0.61
Cluster 3, n= 536 (17.95%)	167.56	0.25	0.17	0.42
Cluster 4, n= 534 (17.89%)	162.73	0.31	0.09	0.40

772 Simpson-based and Nestedness-resultant dissimilarities, ranged 0 to 1. Sørensen-based dissimilarity, not included in LCA
 773 due to multicollinearity (Sørensen-based dissimilarity = Simpson-based dissimilarity + Nestedness-resultant dissimilarity),
 774 is based on after-modelling calculation. (Cluster 1, a pattern with low species richness and a highly unstable structure due to
 775 species replacement. Cluster 2, a transitional pattern with moderate richness. Cluster 3, a diverse pattern with relative stable
 776 species composition. Cluster 4, a pattern with extremely low variations in species composition due to nested species gain or
 777 loss.)
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Table 4. Regression analyses for the association between derived clusters and life expectancy at birth.

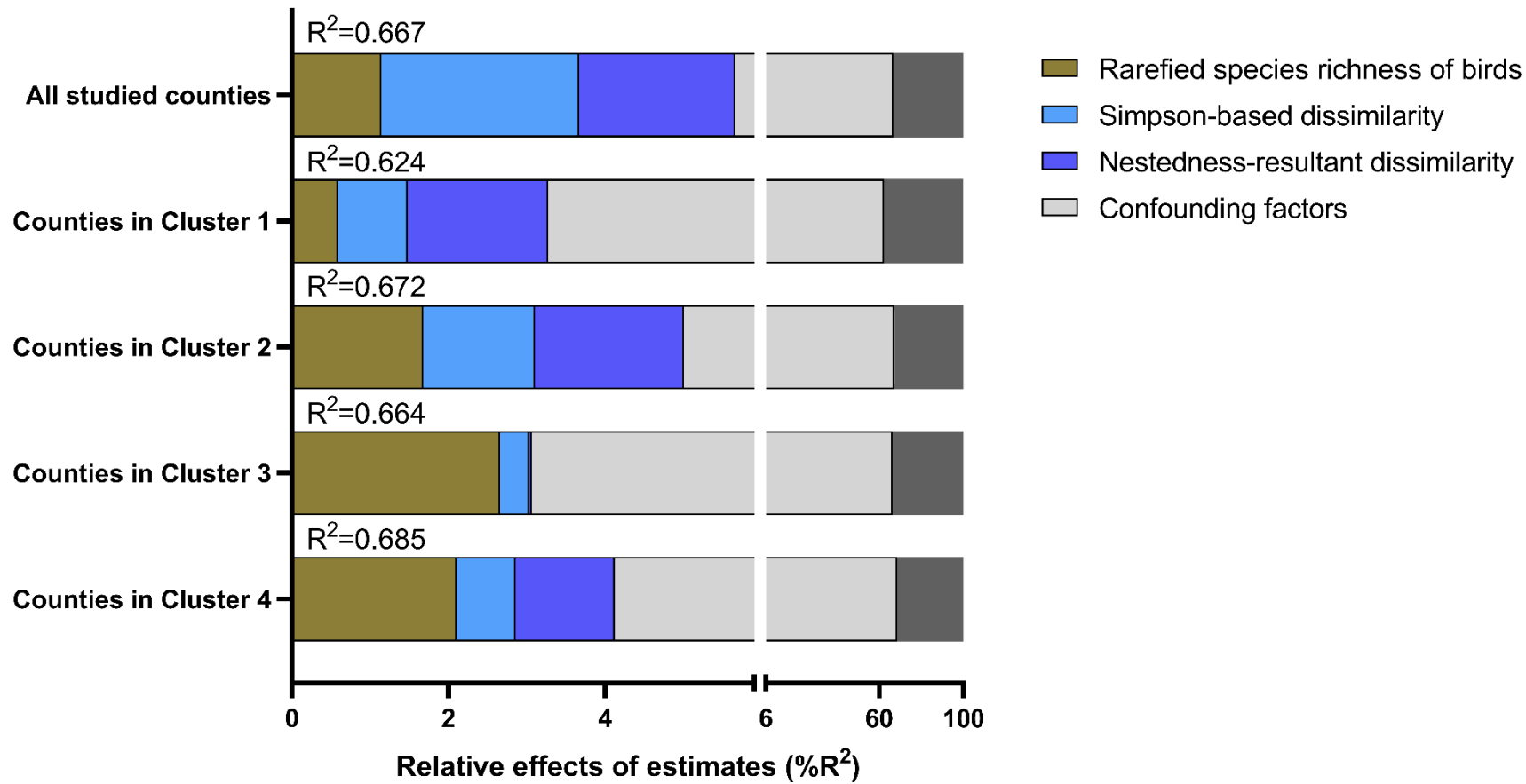
Variables	Life expectancy at birth	
	Regression coefficients (95% CIs)	<i>p</i> value
Biodiversity		
Cluster 1	Reference category	-
Cluster 2	0.200 (0.062, 0.337)	0.004
Cluster 3	0.484 (0.302, 0.665)	0.001
Cluster 4	0.558 (0.383, 0.733)	<0.001
Population information		
Population (per thousand)	0.595 (0.404, 0.787)	<0.001
Male (%)	0.180 (0.152, 0.207)	<0.001
White alone (%)	0.021 (0.017, 0.026)	<0.001
Age ≥ 80 (%)	0.223 (0.175, 0.271)	<0.001
Socio-demographics		
A bachelor's degree or higher (%)	0.129 (0.118, 0.140)	<0.001
Median household income (per thousand US dollars)	0.057 (0.045, 0.070)	<0.001
Unemployment rate, age < 65 (%)	0.027 (0.004, 0.049)	0.020
Poverty rate (%)	-0.086 (-0.107, -0.066)	<0.001
Healthcare		
Health insurance coverage, age < 65 (%)	-0.067 (-0.082, -0.052)	<0.001
Physicians per thousand population	-0.069 (-0.114, -0.024)	0.003
Residential environment		
Rural-Urban Continuum Area Code		
1 Metro areas	Reference category	-
2	0.338 (0.116, 0.560)	0.003
3	0.589 (0.351, 0.828)	<0.001
4	0.326 (0.053, 0.599)	0.019
5	0.362 (0.000, 0.724)	0.050
6	0.362 (0.127, 0.597)	0.003
7	0.356 (0.098, 0.614)	0.007
8	0.478 (0.178, 0.777)	0.002
9 Completely rural	0.529 (0.240, 0.818)	<0.001
Geographic characteristics		
Total area (per thousand square miles)	-0.038 (-0.054, -0.022)	<0.001
Longitude	-0.01 (-0.015, -0.004)	<0.001
Latitude	0.065 (0.050, 0.079)	<0.001
Annual precipitation, inches	-0.001 (-0.006, 0.003)	0.603

780 CIs, Confidence intervals. Based on 2985 studied US counties.

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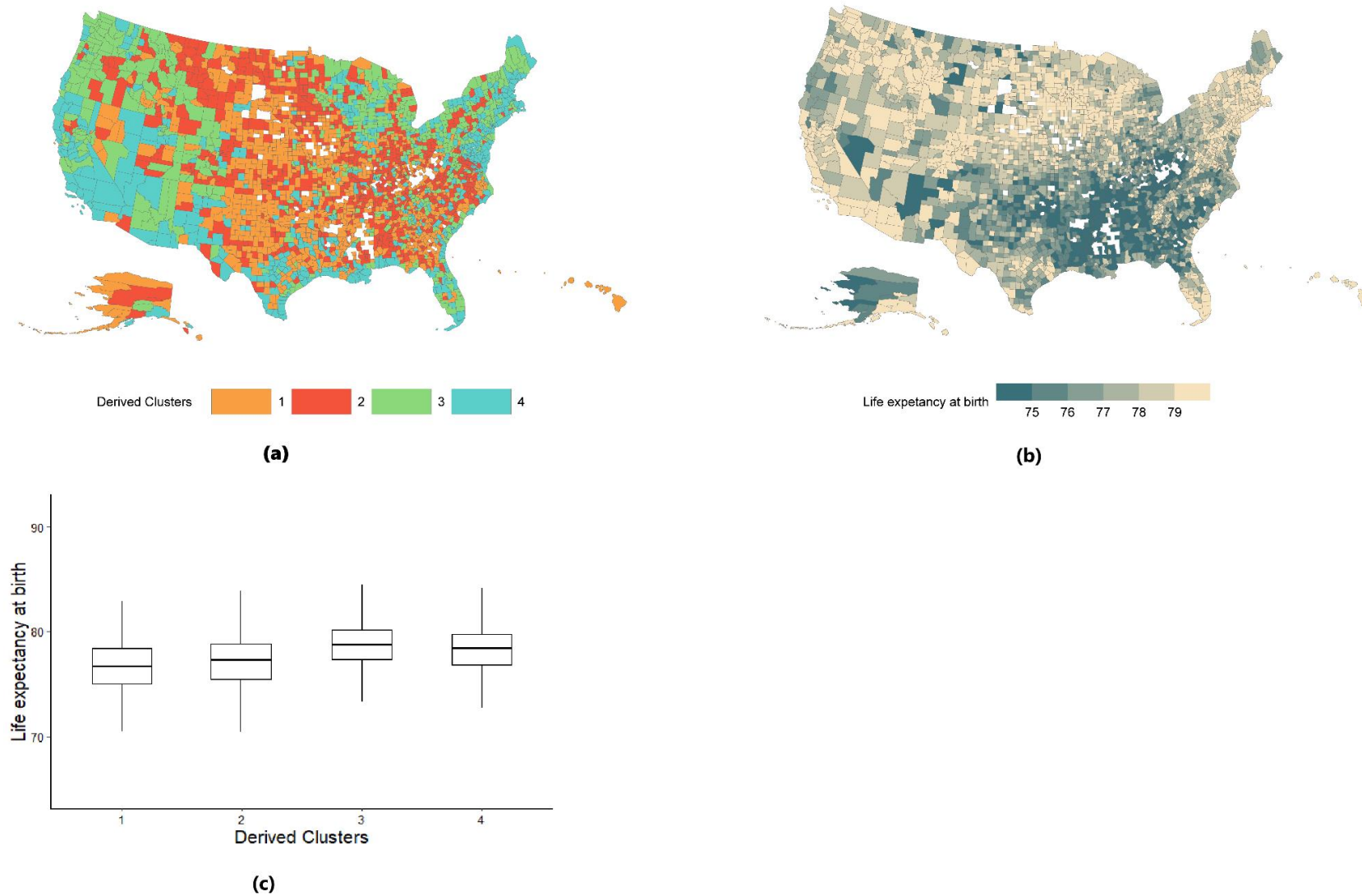
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Figure 3. Variance partitioning analysis results with respect to life expectancy at birth.



All predictors were scaled to interpret parameter estimates on a comparable scale, and variance partitioning results were calculated based on standardized regression coefficients.

Figure 1. The geographical patterns of the clusters and life expectancy across the US. (a) Cluster distribution. (b) Life expectancy at birth in 2019. (c) The Box-plot of life expectancy at birth by identified clusters.



Cluster 1, a pattern with low species richness and a highly unstable structure due to species replacement. Cluster 2, a transitional pattern with moderate richness. Cluster 3, a diverse pattern with relative stable species composition. Cluster 4, a pattern with extremely low variations in species composition due to nested species gain or loss.

Figure 2. Regression analyses for the association between derived clusters and 19 cause-specific mortality rates with adjustments for other potential confounding factors (Cluster 1 as referent). CIs, Confidence intervals. *, **, ***: The number of clusters demonstrated significant difference from Cluster 1.

