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³ Utilizing Hill Numbers to Analyze
⁴ Species Evenness Time Sequences
⁵ Across Multiple Dimensions:

⁶ A Study Based on the Integration of Living Planet
⁷ Index
⁸ and Global Abundance Data for 9700 Birds

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Contents

¹⁷	1 Introduction	4
¹⁸	2 Methods	8
¹⁹	2.1 Global Species Lambda Calculation	8
²⁰	2.2 Data Cleaning	9
²¹	2.3 Data Matching	10
²²	2.4 Abundance Distribution Analysis	11
²³	2.5 Original LPI Calculation	11
²⁴	2.6 Weighted LPI Calculation	12
²⁵	2.7 Effective Diversity Calculation	13
²⁶	2.7.1 Hill number($q=1$) Calculation	13
²⁷	2.7.2 Hill number($q=2$) Calculation	13
²⁸	2.7.3 Evenness Indexes Calculation	13
²⁹	2.8 Evenness Sensitivity	14
³⁰	2.9 Analysis on Different Dimensions of Evenness	14
³¹	3 Results	15
³²	3.1 Overview of Changes in Abundance Distribution	15
³³	3.2 Hypothesis Test about Weighted LPI by Abundance	16
³⁴	3.3 LPIs & Hill Numbers in Different Abundance-based Species Groups	16
³⁵	3.4 Original and Weighted LPIs	17
³⁶	3.5 Hill Number Sequences	17
³⁷	3.6 Relative Evenness Indexes	20
³⁸	3.7 Two Different Dimensions of Species Evenness	20
⁴⁰	4 Discussion	24
⁴¹	4.1 Hypothesis Test about Weighted LPI by Abundance	24
⁴²	4.2 Limitation and Future Work	24
⁴³	4.3 Adjustment for LPI	25
⁴⁴	4.4 Adjustment for Hill number	26
⁴⁵	4.5 Living Planet Indexes	26
⁴⁶	4.6 Hill numbers	27
⁴⁷	4.7 Pielou evenness and $I_p(\lambda)$	28

48	4.8 Evenness Sensitivity Analysis	28
49	4.9 Broader Implications and Future Directions	29
50	5 Data and Code Availability	30

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Declaration

- 52 All data used in this research is publicly available, with the exception of
53 the LPI completeness data, which has not yet been formally published.
54 The datasets mainly originate from the Living Planet Index (LPI). I take
55 full responsibility for the data processing, analysis, and visualization.
56 My supervisor, James Rosindell, offered detailed and patient guidance
57 throughout the project.

Abstract

59 The conservation of biodiversity has garnered significant attention in re-
60 cent years. Quantifying species diversity provides a robust theoretical
61 foundation for formulating biodiversity conservation policies. Hill num-
62 ber and living planet index(LPI) are both robust indicators for commu-
63 nity's development. In this research, I aimed to comprehensively eluci-
64 date species diversity trends of birds in global scale by integrating Hill
65 numbers with a weighted LPI by global abundance. I estimated global
66 abundance development by combining a global abundance dataset of
67 9,700 birds with the dataset about species growth generated during the
68 Living Planet Index calculation process. Furthermore, I conducted analy-
69 sis on abundance distribution based on combined dataset and calculation
70 of evenness sensitivity based on Hill number. This multifaceted approach
71 offers a more nuanced understanding of biodiversity dynamics especially
72 in terms of species evenness, potentially informing more complete global
73 biodiversity monitoring where data are available.

74 **Keywords:** Biodiversity, Hill Numbers, Living Planet Index, Species
75 Evenness, Global Abundance

76 1 Introduction

77 The biological diversity of ecosystems has always attracted the atten-
78 tion of environmentalists and ecologists (Wilson 1995). In recent decades,
79 global biodiversity has been decreasing and extinction rates of species are
80 much higher than background rates (Chaytor et al. 2002). Key biodiver-
81 sity indicators such as species' population trends, extinction risk, habitat
82 extent and habitat condition show a downward trend (Butchart et al.
83 2010). The Convention on Biological Diversity (CBD) illustrates targets
84 for a global effort on biodiversity conservation, sustainable utilization,
85 and equitable benefit-sharing (Rosendal 2000). The objective of CBD
86 in 2010 is to preserve ecosystem services, uphold the well-being of the
87 earth, and guarantee that crucial advantages are accessible to all indi-
88 viduals and the environment(CBD 2010). Most countries, however, failed
89 to meet the targets of CBD's 'Strategic Plan for Biodiversity 2011–2020'

90 (Buchanan et al. 2020). Then, CBD's vision for the future was articu-
91 lated, emphasizing that biodiversity should not only be valued but also
92 conserved, restored, and utilized in a sustainable manner.(Joly 2022).
93 Biodiversity is the sum total of all biotic variation from the level of genes
94 to ecosystems (Purvis & Hector 2000). Biodiversity is a broad and com-
95 plex concept that is difficult to quantify directly, so researchers often
96 use appropriate surrogate indicators when analysing biodiversity(Sarkar
97 2002). Species diversity is an indicator that is relatively easy to quali-
98 fied and its main factors are species evenness and species richness. The
99 richness is a measure of the number of different species present in a par-
100 ticular area or ecosystem while species evenness originally refers to the
101 uniformity of the abundance distribution among different populations
102 within a community. Even when species richness remains unchanged or
103 changes only a little, evenness can fluctuate where the abundances of
104 dominant species fluctuate significantly over time. Evenness has been
105 shown to exhibit a significant linear relationship with total biomass when
106 richness level remains nearly constant over time(Wilsey & Potvin 2000).
107 Richness and evenness are both regarded as important indicators for di-
108 versity at first but species richness has been more frequently used among
109 diversity indicators because of its high accessibility to the public and to
110 policy makers and researchers often restrict consideration of diversity to
111 only species richness (Andelman & Willig 2003). A research about prin-
112 cipal components analysis(PCA) for different biodiversity indexes showed
113 that different indices including richness, evenness performed distinctively
114 on two main principal components of diversity in different sampling sites
115 after dimension reduction, which means that these indicators cover dif-
116 ferent aspects and actually, species richness could not fully represent the
117 biodiversity(Wilsey et al. 2005). So it has been suggested that species
118 evenness is a main factor of species diversity as well and the indices for
119 species richness should be combined with it to represent the effective di-
120 versity(Tuomisto 2010).
121 To monitor progress towards the CBD's 2050 goals, it is important to put
122 forward appropriate quantitative measures of global biodiversity(Chandra
123 & Idrisova 2011). Hill number is an excellent index for measuring effec-
124 tive species diversity that is widely used in ecology. It can take into ac-

125 count both the species richness and evenness of certain community and
126 can adjust the sensitivity of species diversity to the relative abundance
127 of species by adjusting the q value according to the characteristics of the
128 species composition in the communityChao et al. (2014). Shannon In-
129 dex and Simpson Index are both widely used types of diversity measure-
130 ment and Hill number is exponential result of Shannon entropy when q
131 value equals 1 while it is the inversion of Simpson Index when q equals
132 2 (Keylock 2005). It could generally represent diversity rather than fo-
133 cusing on a single factor concerning diversity. Regardless of how the p-
134 value is adjusted, the Hill number remains influenced by species richness
135 during the calculation process and can only capture changes in species
136 evenness(Mouillot & Wilson 2002). The calculation of Pielou evenness is
137 more independent with species richness(Gosselin 2006) and it is based on
138 the Shannon index as well. Hill number is a practical and robust mea-
139 surement of species diversity, but constructing diversity time sequences
140 via Hill numbers requires relative abundance data for most species in the
141 group over time, which is often difficult to obtain. As a result, there is
142 a lack of data to enable Hill number analyses through time and study
143 change at the global scale.

144 The Living Planet Index (LPI) is another widely utilized resource in bio-
145 diversity studies. The Living Planet Index (LPI) is an index with asso-
146 ciated metrics that tracks population trends across numerous species in
147 diverse ecosystems. Its methodology involves calculating the growth rates
148 of each population's abundance over time, referred to as lambda values.
149 These lambda values represent the growth multiple of each population
150 based on the Living Planet Dataset (LPD). So LPI is obtained based
151 on solid data foundation concerning abundance time sequences of large
152 number of populations in global scale. First, lambda values are calcu-
153 lated for each population, and then averaged across all populations of the
154 same species within each realm after standardization. The time sequences
155 of species lambda values in different realms are then used as exponents
156 in a cumulative multiplication calculation, starting from 1 in the base
157 year, to derive the relative index sequences for each realm and system.
158 LPI is used as an index to illustrate the general trend in changes in the
159 community's total biomass, which in turn indicates potential changes in

160 species diversity (Loh et al. 2005). Consequently, LPI has become widely
161 accepted because it is simple to calculate and covers abundance time se-
162 quences of global populations of many species.
163 Relative abundances of species are a critical factor in evenness (Tuomisto
164 2010). In addition, total biomass of a community has been shown in
165 some cases to have a significant positive correlation with its diversity(Bock
166 et al. 2007) and it is determined by species richness and their abundances.
167 As an indicator for species diversity, species richness in certain is simple
168 to calculate but it disregards the effect of abundance(MacArthur 1965).
169 As previously mentioned, species abundances are closely related to the
170 primary factors influencing species diversity concerning species even-
171 ness and community size. The Living Planet Index (LPI) indirectly links
172 to species diversity through the overall trend in community's biomass.
173 Thus, it is beneficial for the LPI to incorporate relative abundance data
174 for each species to more accurately reflect their contributions because
175 the biomass has direct linear relationship with species abundance (Hall-
176 mann et al. 2021). This could be achieved by calculating weighted av-
177 erage species lambda time sequences based on relative abundance. A
178 previous research also showed that employing appropriate indicators for
179 weighting when calculating the LPI can somewhat address the shifting
180 pattern of biodiversity(Buschke et al. 2021). If this weighting process is
181 applied, there is a hypotheses remain to be tested whether species abun-
182 dance has significant positive relationship with its growth potentiality.
183 Moreover, the LPD uses 2476 units for species's abundances correspond-
184 ing to various methods used by its sources for collecting data and con-
185 verting between different units can be extremely challenging. As a result,
186 there is no unified unit for abundance and no effective weighting by rel-
187 ative abundance can be done in the process of calculating the average
188 of species lambda of in each realm and the species lambda sequences in
189 each realm in LPI calculation are actually not comparable. This presents
190 an opportunity to enhance the LPI by incorporating the effects of rela-
191 tive abundance. Addressing this aspect could improve the LPI's ability to
192 more effectively reflect potential changes in effective biodiversity.
193 In this research, I referred to a dataset of 9,700 birds' global abundance
194 which is based on e-bird dataset from 2010 to 2019(Callaghan et al. 2021)

and combined it with species lambda dataset to create a dataset of estimated global abundance time sequences for birds so that I could solve the problem that there is no consistent unit of abundance in LPD. This combined dataset serves as a foundation for calculating both a weighted Living Planet Index (LPI) based on relative abundance and Hill numbers. Although the species lambda dataset does not indicate any extinctions and bird richness levels have remained relatively stable across time, multi-dimensional analysis of species evenness can still be conducted derived from Hill number calculations.

2 Methods

All of the data analyses are accomplished using R version 4.3.1(R Core Team 2023). Generally, I conducted data cleaning for species lambda dataset in order to raise its effectiveness. This birds' abundances dataset is in global scale, so it should be analysed together with dataset of species lambda time sequences so that I could get species global abundance times sequences. After that, I calculated weighted LPI by abundance and Hill number. Moreover, I conducted relative evenness calculation and evenness sensitivity analysis based on the result of Hill number calculation. The overview of research flow could be found in (Figure 1).

2.1 Global Species Lambda Calculation

The growth rate sequence of each population is calculated firstly to prepare getting species lambda sequences.

$$d_{ijt} = \log_{10} \left(\frac{N_{ijt}}{N_{ij(t-1)}} \right) \quad (1)$$

The d_{ijt} value stands for lambda value of the j-th population of the i-th species, which means its growth rate in year t and the N_{ijt} value stands for the abundance value in this year for j-th population in LPD.

$$\bar{d}_{it} = \frac{1}{m_t} \sum_{j=1}^{m_t} d_{ijt} \quad (2)$$

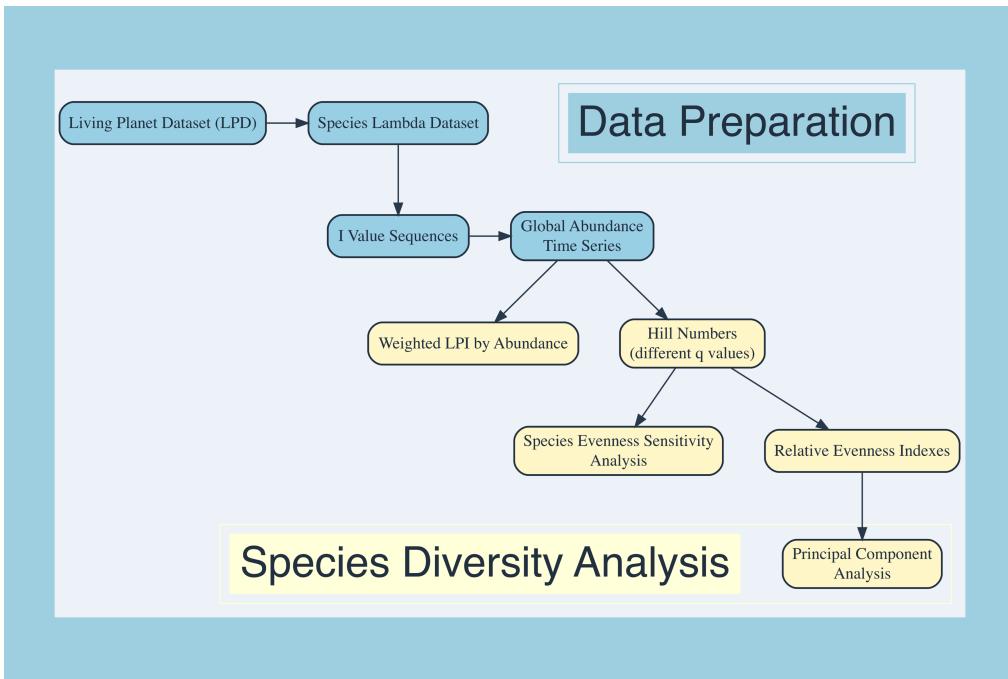


Figure 1: Flowchart of the project including two periods concerning data preparation and species diversity analysis.

220 The d_{it} values stands for lambda values for certain species in year t, which
 221 is the arithmetic mean of lambda values of all populations for this species
 222 in this year and the m_t stands for the number of populations of the i-th
 223 species of which the lambda value in year t is not null.
 224 In the calculation of growth rates, this chain method is frequently em-
 225 ployed for cumulative calculations (Loh et al. 2005).

226 2.2 Data Cleaning

227 These selection standards including the proportion of null values, the rep-
 228 resentative of all populations in global scale according to the percentage
 229 values in LPI completeness data and different species' global abundance
 230 sizes.
 231 Aiming at filtering species lambda sequences to find those with less null
 232 values and determining the starting and ending time points for all se-
 233 quences, I computed the proportion of null values separately for each
 234 species sequence and time column in the dataset of species lambda. Af-
 235 ter fitting a normal distribution, I retained the species (rows) and year

236 (columns) in species lambda dataset with proportions of null values be-
 237 low the mean.
 238 Additionally, I made another selection of species lambda dataset to iden-
 239 tify species encompassing populations that could comprise more than
 240 25% of their global distribution in accordance with proportion val-
 241 ues in LPI completeness data. This adjustment aims to mitigate biases
 242 and enhance the representation of the original dataset.
 243 Moreover, I created five distinct abundance-based species groups: those
 244 with global abundances above the top 25%, above the top 50%, below
 245 the bottom 50%, below the bottom 25%, and within the central 50%.
 246 These groups correspond to the dominant species group, less dominant
 247 species group, less rare species group, rare species group, and middle
 248 species group, respectively. This selection was intended to provide a data
 249 foundation for calculating LPIs, Hill numbers, and other indices for both
 250 common and rare species.

251 **2.3 Data Matching**

252 Firstly, I have made a correction for birds' scientific names in both of
 253 them using the rotl package(Michonneau et al. 2016) in order to match
 254 LPD and birds dataset better based on the scientific names of birds in
 255 them.

$$I_{it} = I_{i(t-1)} \times 10^{d_{it}} \quad (3)$$

256 The I_{it} value stands for the I value of the i-th species in year t. The I
 257 value basically starts from 1, determined by I value and species lambda
 258 value in previous years. So I value sequence follows cumulative calcula-
 259 tion. I computed the I value sequence for each species and subsequently
 260 determined the geometric mean of values across all time points. The I
 261 value sequence is cumulative calculation of abundance trends and the
 262 ratio between averaged I values and global abundance shows the dispar-
 263 ity in magnitude between them. I applied a multiplication factor to the
 264 annual values within the respective I sequence, by utilizing the aforemen-
 265 tioned ratio to estimate a global abundance time sequences for each bird
 266 that are necessary for calculating Hill numbers (Jost 2006). In addition,

²⁶⁷ all I values are positive, making it possible for conducting this data scal-
²⁶⁸ ing for all species.

$$\text{Averaged I-i Value} = \exp\left(\frac{1}{n} \sum_{n=1}^n \log(I_{it})\right) \quad (4)$$

²⁶⁹ The n values stand for the number of time points.

$$\text{Abundance}_{it} = I_{it} \times \left(\frac{\text{Global Abundance}}{\text{Averaged I-i Value}} \right) \quad (5)$$

²⁷⁰ 2.4 Abundance Distribution Analysis

²⁷¹ First, I applied a base-2 logarithmic transformation to the obtained global
²⁷² abundance sequences, resulting in a time series of abundance octave data(Hubbell
²⁷³ 2001). Moreover, I calculate the standard deviation of different abundance-
²⁷⁴ based species groups' abundance octave distribution in each year to show
²⁷⁵ the change of evenness level in one aspect.

²⁷⁶ 2.5 Original LPI Calculation

²⁷⁷ The average d_t and I_t time series for all of these populations were com-
²⁷⁸ puted, following the standard procedure for calculating LPI values.

$$\bar{d}_t = \frac{1}{n_t} \sum_{i=1}^{n_t} d_{it} \quad (6)$$

²⁷⁹ In the computation of the original LPI, an arithmetic average was em-
²⁸⁰ ployed to determine the mean d_t value. The d_{it} is the growth rate of the
²⁸¹ i-th species in year t. The n_t stands for the number of not null average
²⁸² species lambda values in year t.

$$I_t = I_{t-1} \times 10^{\bar{d}_t} \quad (7)$$

²⁸³ A cumulative multiplication operation is then applied. The outcomes of
²⁸⁴ calculation are mainly determined by the average species lambda in each
²⁸⁵ year. The I_t values are actually relative values initiating with a stan-
²⁸⁶ dard value of 1. In the step of data matching, the I value sequence would
²⁸⁷ show the trend in the change of abundance of certain population while in

288 the calculation of original LPI, this cumulative calculation is applied to
289 present overall trends in total biomass of certain groups of species.

290 **2.6 Weighted LPI Calculation**

291 In the weighted LPI calculation, the weighting process involves calculat-
292 ing the weighted average of species' lambda values. I proposed a hypoth-
293 esis regarding the biological significance of this weighting process and
294 tested it by fitting a generalized linear model (GLM).

295 The metabolic rate of certain species is strongly correlated with both
296 body size and ambient temperature (Brown et al. 2004). This research of
297 brown also demonstrates a significant linear relationship between metabolic
298 rate and individual biomass production. Moreover, the maximum growth
299 rate of a species is typically scaled by its metabolism, as reproduction is
300 driven by metabolic processes. Finally, I used the R function 'glm' to
301 establish a relationship between maximum species lambda value with
302 global abundance data and other factors in my research, guided by in-
303 sights from previous research on metabolic theory. To incorporate metabolic
304 information into species lambda sequences, I used the maximum species
305 lambda value as a proxy for metabolic rates. I also used the arithmetic
306 mean of latitude data from global populations in the LPD to represent
307 temperature factors. Additionally, I employed global abundance devel-
308 opment to represent biomass production and referenced to species body
309 mass data(Morales-Castilla et al. 2012) to link the obtained variances
310 with corresponding variances in metabolic theory.

311 The weighting process in averaged species lambda calculation followed
312 another formula. The P_{it} value represents the relative abundance data of
313 the i-th species in year t.

$$\bar{d}_t = \sum_{i=1}^{n_t} d_{it} \times P_{it} \quad (8)$$

₃₁₄ **2.7 Effective Diversity Calculation**

₃₁₅ **2.7.1 Hill number(q=1) Calculation**

$$^1D_t = \exp \left(- \sum_{i=1}^S P_{it} \ln(P_{it}) \right)$$

₃₁₆ The 1D_t values represent the exponential form of Shannon Index values
₃₁₇ in year t while the P_{it} values denote the relative abundance of the i-th
₃₁₈ species in year t.(Bromiley et al. 2004)

₃₁₉ **2.7.2 Hill number(q=2) Calculation**

₃₂₀ In my research, species richness almost remain unchanged during given
₃₂₁ period of time in each abundance-based species group, so evenness has
₃₂₂ large influence on the change of diversity. Therefore, I calculated Hill
₃₂₃ numbers with q values of 1 and 2 separately, aiming to provide a founda-
₃₂₄ tion for analyzing species evenness while also quantifying species diversity
₃₂₅ across different abundance-based species groups. 2D_t value represents the
₃₂₆ inversion of Simpson Index value in year t.

$$^2D_t = \sum_{i=1}^S P_{it}^2 \quad (9)$$

₃₂₇ **2.7.3 Evenness Indexes Calculation**

₃₂₈ Pielou evenness is an robust evenness index that its calculation is rela-
₃₂₉ tively independent from species richness(Jost 2010). This method aims
₃₃₀ to assess the extent to which the distribution of species abundances devi-
₃₃₁ ates from perfect evenness, thereby serving as the relative evenness index
₃₃₂ of certain community(Studeny et al. 2011). In the calculation of Pielou
₃₃₃ evenness, H_t values refer to Shannon Index value in year t and J_t values
₃₃₄ represent the Pielou evenness in year t while S_t values stand for species
₃₃₅ richness level in this year.

$$H_t = - \sum_{i=1}^S P_{it} \ln(P_{it})$$

$$J_t = \frac{H_t}{\log(S_t)} \quad (10)$$

336 There is another index of evenness based on Hill number and have similar
 337 mathematical principles to Pielou evenness. A previous research proposed
 338 a new method to measure relative evenness based on the likelihood ratio
 339 G, Pearson's X2 and Hill number(Cressie & Read 1984, Read & Cressie
 340 2012).

$$I_{p,t}(\lambda) = \frac{1}{\lambda(\lambda + 1)} \left[\left(\frac{N(0)_t}{N(\lambda + 1)_t} \right)^\lambda - 1 \right] \quad (11)$$

341 Here, $I_{p,t}(\lambda)$ serves as an index to measure the degree of deviation, where
 342 higher values indicate lower levels of relative evenness. The $I_{p,t}$ value rep-
 343 resents the relative evenness level in year t , while λ refers to the weight
 344 assigned to dominant species. $N(0)_t$ and $N(\lambda + 1)_t$ represent the Hill
 345 numbers in year t when q equals 0 and $\lambda + 1$, respectively.

346 2.8 Evenness Sensitivity

347 I calculated growth rate at each time point of each Hill number sequence
 348 and I measured the degree of changes in grow rates when the q value in-
 349 creased from 1 to 2 by calculating the absolute value of ratio between
 350 the changing rates of the Hill number at $q = 1$ and that of the Hill num-
 351 ber at $q = 2$ at each time point. This indicator shows how the ability
 352 of species evenness to influence species diversity would change when the
 353 weight of richness decreases and that of evenness grows in each abundance-
 354 based species group, which means the evenness sensitivity to species
 355 evenness.

$$\text{Evenness Sensitivity}(t) = \left| \frac{\frac{d^2 D_t}{dt^2}}{\frac{d^1 D_t}{dt}} \right| \quad (12)$$

356 2.9 Analysis on Different Dimensions of Evenness

357 I calculated arithmetic mean of evenness sensitivity, the arithmetic mean
 358 of standard deviation in different abundance-based species groups' abun-
 359 dance distribution and arithmetic mean of these groups $I_p(\lambda)$ in all year

360 range. When calculating both $I_p(\lambda)$ and Pielou evenness time sequences,
 361 I largely mitigated the influence of species richness on evenness. However,
 362 the potential ecological interaction between evenness and other biodiver-
 363 sity factors remains uncertain. To determine if ecological connections ex-
 364 ist between species evenness and other factors of species diversity, and to
 365 identify the specific dimension of evenness where these connections may
 366 reside, I conducted Generalized Linear Model(GLM) fitting on different
 367 abundance-based species groups' $I_p(\lambda)$ with their SD of abundance distri-
 368 bution and evenness sensitivity over time.

369 **3 Results**

370 **3.1 Overview of Changes in Abundance Distribu-** 371 **tion**

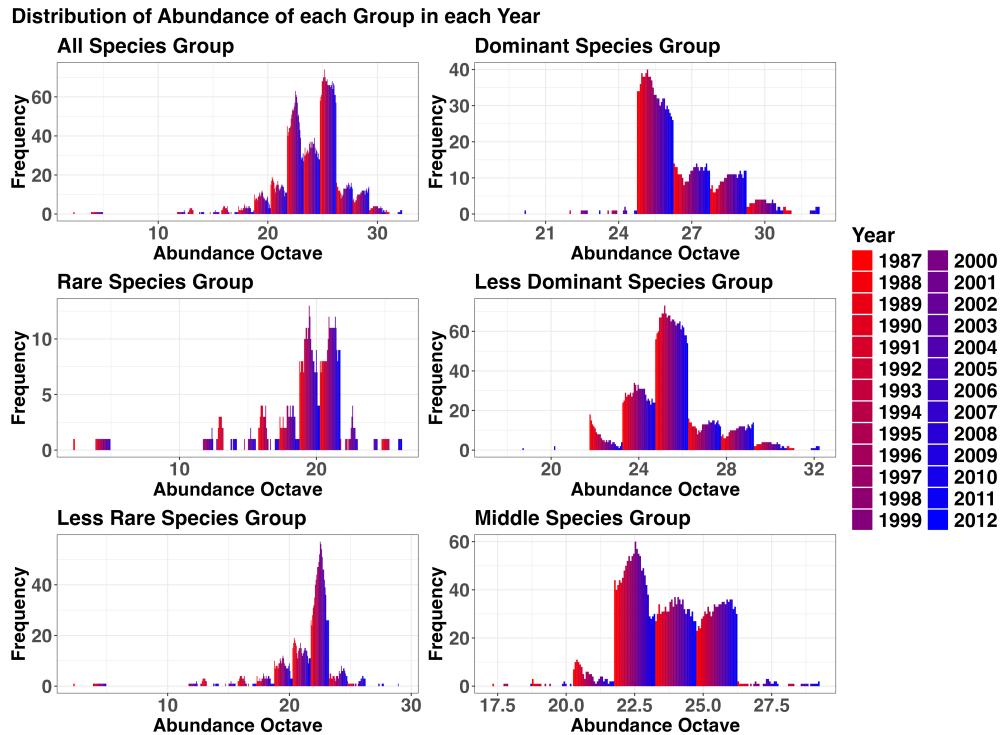


Figure 2: The frequency distribution of species across different abundance octaves, based on the logged abundances within various abundance-based species groups for each year. Different colors represent different years.

372 In six different abundance-based species groups, the abundance distribu-
 373 tion of each group changes greatly over time(Figure 2) and each abundance-
 374 based species group mainly consists of proportionally more common species
 375 compared to previous studies (Loh et al. 2005, McRae et al. 2017). Even
 376 in the rare species group, the abundance octave with most species is over
 377 20.

378 **3.2 Hypothesis Test about Weighted LPI by Abun-**
 379 **dance**

Maximum Growth Rate = - 0.168641

$$\begin{aligned}
 & + 0.021672 \times \log(\text{Body Mass}) \\
 & + 0.018891 \times \log(\text{Global Abundance}) \\
 & - 0.002928 \times \text{Latitude}
 \end{aligned} \tag{13}$$

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-0.168641	0.091022	-1.853	0.064901
log(Body.Mass.gram.)	0.021672	0.005148	4.210	3.38×10^{-5} ***
log(global_abundance)	0.018891	0.005312	3.556	0.000437 ***
Latitude	-0.002928	0.000640	-4.575	6.99×10^{-6} ***

*Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1*

Dispersion parameter for gaussian family taken to be 0.03030405

Null deviance: 10.3391 on 302 degrees of freedom

Residual deviance: 9.0609 on 299 degrees of freedom

AIC: -193.58

Number of Fisher Scoring iterations: 2

Table 1: GLM Model Fitting Results

380 The residual deviance of the model, with 299 degrees of freedom, is 9.0609,
 381 suggesting a good fit for the GLM. The coefficient's p-value for the term
 382 log(global_abundance) is 0.000437, indicating a significant positive corre-
 383 lation between the max species lambda value and global abundance(Figure 4).

384 **3.3 LPIS & Hill Numbers in Different Abundance-**
 385 **based Species Groups**

386 In order to compare the overall trends of Hill numbers with LPIS in each
 387 abundance-based species group and measure degrees of their changes, I

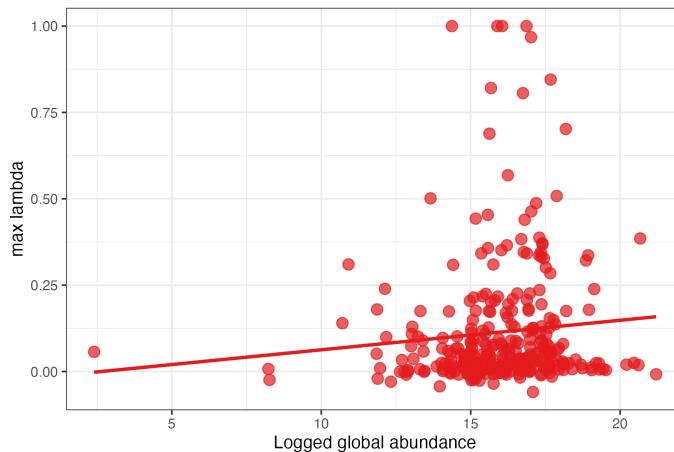


Figure 3: Hypothesis Test for Abundance’s Influence on Species’ Growth

scaled their index values so that the initial values are all set to 1, so values of each index are not comparable with each other except weighted LPI by abundance and original LPI. The divergence of these 2 LPIS is not very obvious in most species groups except for all species group and dominant species group. Furthermore, LPIS have quite different trends with other indexes in dominant species group. From the aspect of the development trends, Hill numbers with different q values generally exhibit a trend of initially rising and then falling in all abundance-based groups. Additionally, Hill number shows more dramatic changes when q equals 2 compared with Hill number($q=1$).

3.4 Original and Weighted LPIS

The main difference between these two sets of lines lies in their degrees of fluctuation, with the weighted LPI lines exhibiting more pronounced volatility. Additionally, in the original LPI lines, growth rate values are positive in most years for all groups except rare species group. In contrast, the weighted LPI lines show a greater occurrence of negative growth rate values

3.5 Hill Number Sequences

When q equals 1, Hill number values of the middle species were the highest, while the minimum values appeared in index of the rare species group.

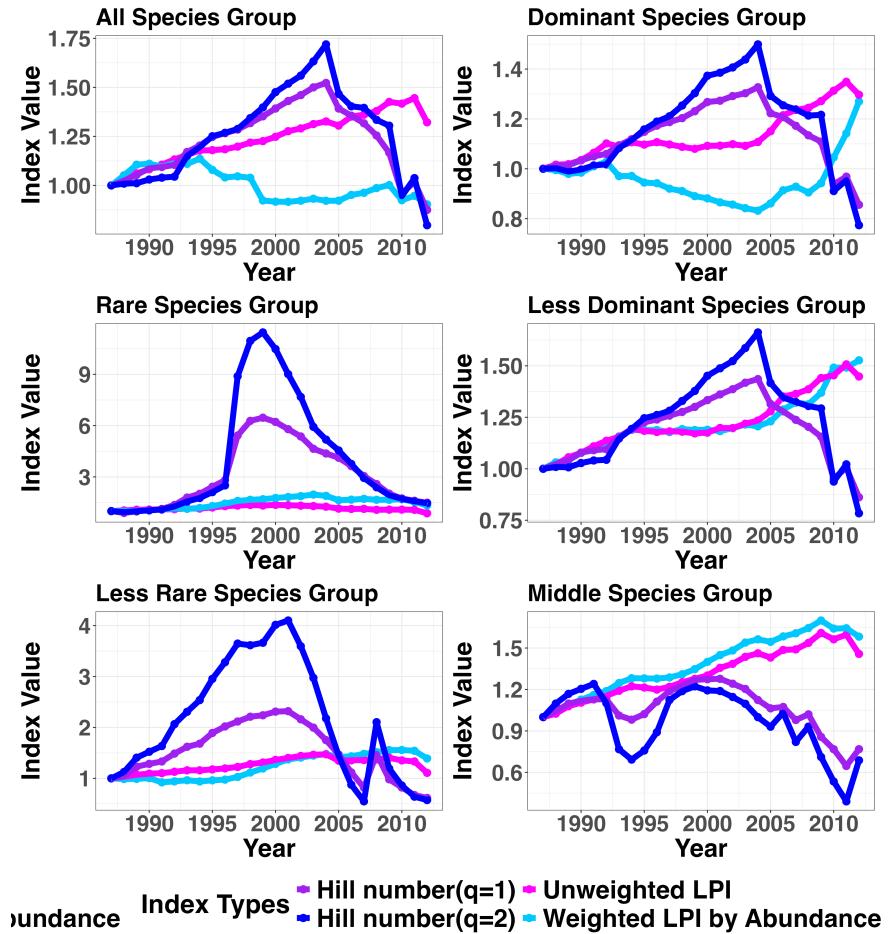


Figure 4: Line chart of different indexes sequences in different abundance-based species groups. Lines in different colors represent different types of indexes including weighted LPIS, original LPIS, Hill numbers($q=1$) and Hill numbers($q=2$).

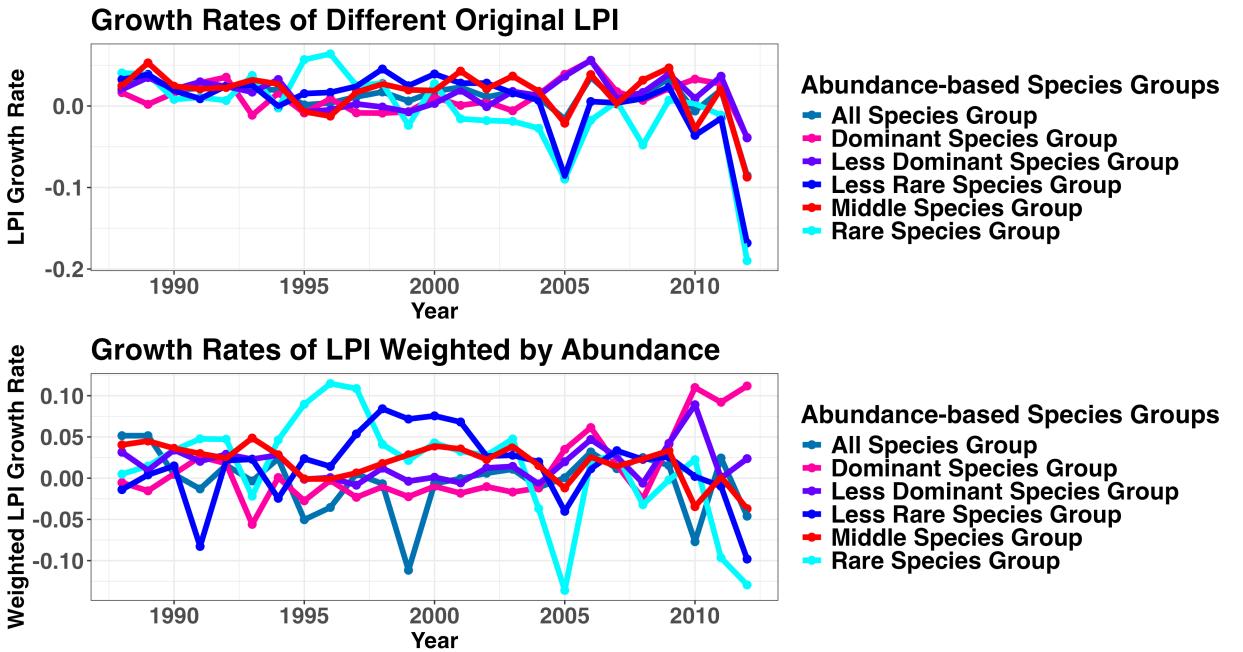


Figure 5: Lines of original LPIs' and weighted LPIs' growth rate time sequences.

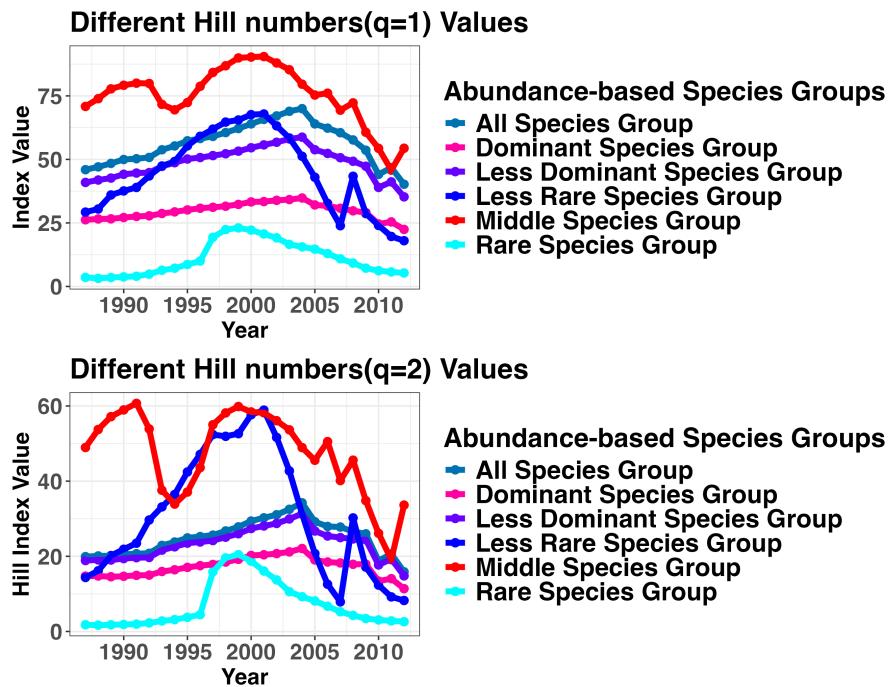


Figure 6: Top subplot: Lines of Hill number($q=1$). x axis: Year. y axis: Index Value. Bottom subplot: Lines of Hill number($q=2$).

408 The relative sizes of indexes values of six different abundance-based species
409 groups change greatly after the q value of Hill number increased. When
410 I increased the q value from 1 to 2, values of every sequence dropped by
411 different degrees. Furthermore, the highest values and the second high-
412 est values exist in index of middle species group or less dominant species
413 group. In terms of Hill numbers' development tendencies, sequences of
414 middle species group or less dominant species group fluctuated more dra-
415 matically, whereas other sequences were relatively stable. In Figure 4,
416 all Hill number sequences were scaled for comparison with LPI trends,
417 meaning the displayed trends do not reflect their actual patterns. In Fig-
418 ure ??, the Hill number trend was adjusted, resulting in much more sta-
419 ble sequences across all species groups, including dominant, rare, and less
420 dominant species groups.

421 **3.6 Relative Evenness Indexes**

422 In terms of Pielou evenness, intense changes in index values only occur in
423 the rare species group and the less rare species group. Values of Pielou
424 evenness in the middle species group are the highest at most time points
425 while the lowest values of Pielou evenness regularly exists in rare species
426 group. The evenness rankings of the abundance-based species groups, as
427 indicated by $I_p(\lambda)$, closely align with their rankings according to Pielou's
428 Evenness Index. Moreover, general trends of $I_p(\lambda)$ sequences with differ-
429 ent λ values are similar to each other and fluctuations in $I_p(\lambda)$ are much
430 larger than those in Pielou Evenness in all groups Figure 7. Moreover,
431 there is almost no change occurring in trends of $I_p(\lambda)$ sequences when λ
432 value changes.

433 **3.7 Two Different Dimensions of Species Evenness**

434 The abundance distribution serves as one dimension of relative evenness
435 in this research while different abundance-based species groups sensitivity
436 to evenness is regarded as another dimension of relative evenness. The
437 standard deviation in abundance distribution across different abundance-
438 based species groups does not follow the same trend with these groups'
439 $I_p(\lambda)$ sequences. The most even abundance distribution exists in domi-

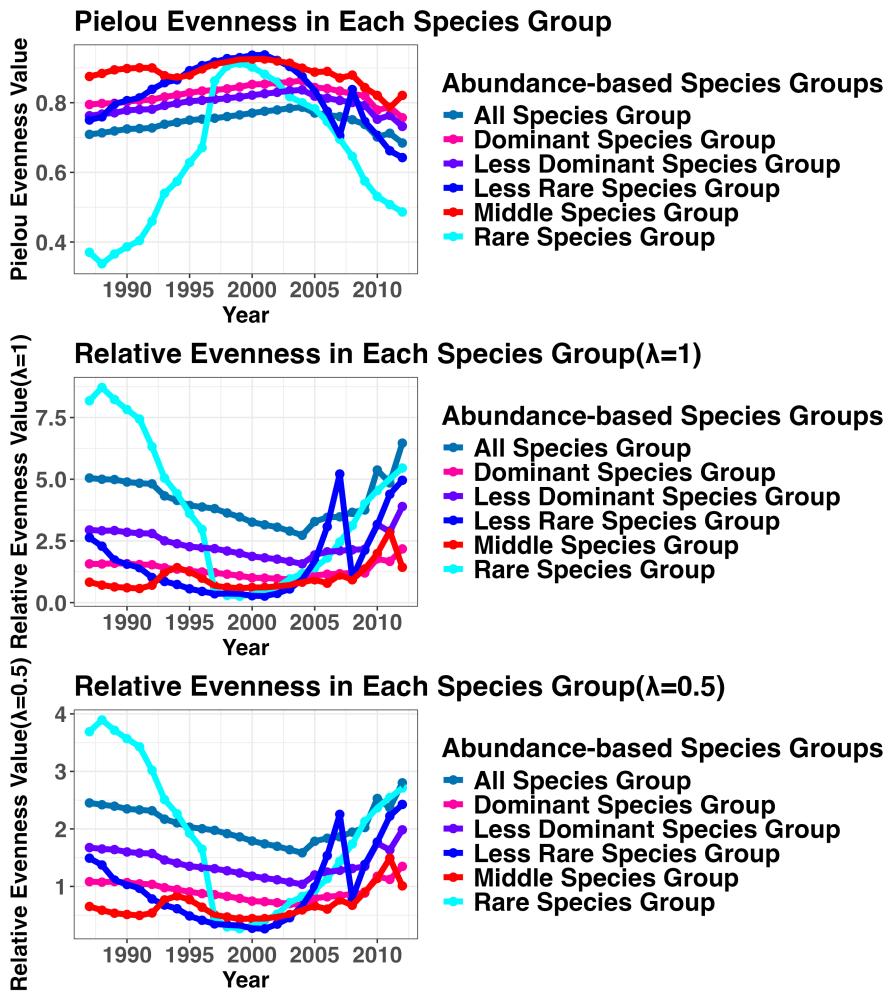


Figure 7: Top subplot: Lines of Pielou Evenness. Middle subplot: Lines of $I_p(\lambda)(\lambda=1)$. Bottom subplot: Lines of $I_p(\lambda)(\lambda=0.5)$.

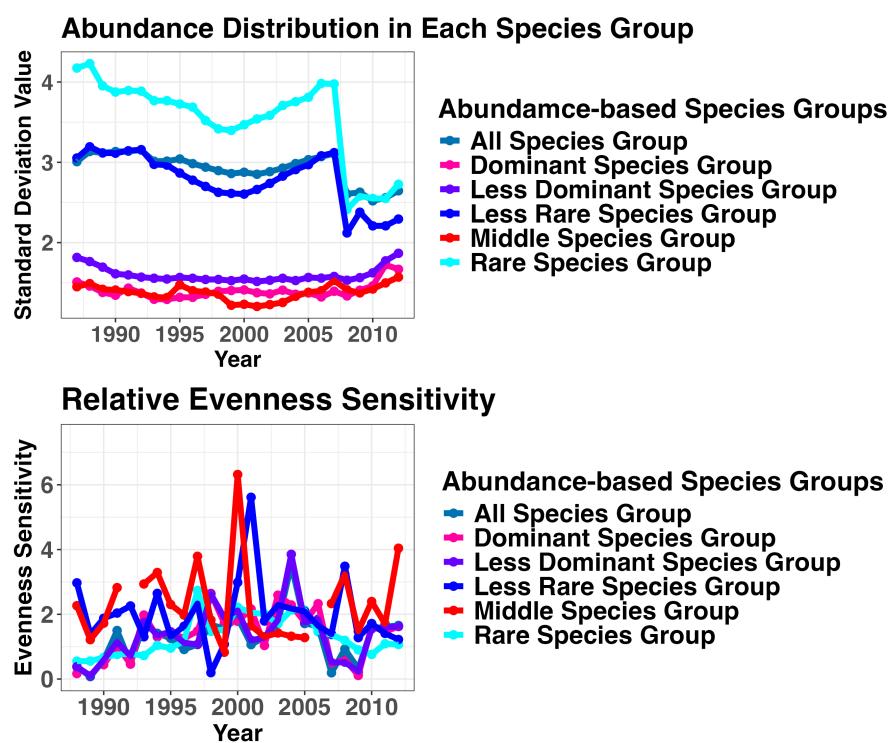


Figure 8: Top subplot: Lines of SD in Abundance Distribution in Each Abundance-based Group. Bottom subplot: Lines of Evenness Sensitivity.

440 nant species group, less dominant species group or middle species group.
 441 Concurrently, the highest sensitivity to evenness regularly exists in less
 442 rare species group at some time points(Figure 8). Results of the statis-
 443 tical analyses also indicate that average relative evenness, average SD
 444 of abundance distribution and average sensitivity to evenness over time
 445 do not follow the same trend within different abundance-based species
 446 groups. The Average standard deviation of less rare species group over
 447 time is large but its average sensitivity to evenness and average relative
 448 evenness level across time are relatively high.

Species Groups	Average $I_p(\lambda)(\lambda=1)$ Value	Average SD of Abundance Distribution	Evenness Sensitivity
All Species	4.08	2.93	1.27
Top 25%	1.32	1.40	1.68
Bottom 25%	3.66	3.54	1.32
Top 50%	2.38	1.60	1.37
Bottom 50%	1.63	2.79	2.00
Middle 50%	0.99	1.38	5.72

Table 2: Two Different Dimensions of Relative Evenness Concerning Abundance Distribution and Sensitivity to Evenness in Different Abundance-based Species Groups

449 In the fitting outcome of GLM in different abundance-based species groups,
 450 two terms concern evenness sensitivity and abundance distribution. The
 451 fitting results indicate that the coefficient for abundance distribution is
 452 significant (with low p-values) in abundance-based species groups that
 453 have a small average standard deviation of abundance distribution. In
 454 terms of the coefficients of evenness sensitivity, all of the p-values do not
 455 reach significant level except the p-value for this coefficient in less domi-
 456 nant species group.

P-values for the coefficients of the various terms	All Species Group	Dominant Species Group	Dom- inant Species Group	Rare Species Group	Less Rare Species Group	Middle Species Group
Evenness Sensi- tivity	0.10	0.80	3.33×10^{-8}	0.13	0.17	0.53
Abundance Dis- tribution	0.35	0.030	0.19		1.16×10^{-6}	0.022

Table 3: Outcome of GLM Fitting on Relative Evenness($I_p(\lambda)$) with Sensitivity to Evenness and SD in Abundance Distribution across different abundance-based species groups

457 4 Discussion

458 4.1 Hypothesis Test about Weighted LPI by Abun- 459 dance

460 The GLM results, which modeled maximum species lambda using species'
 461 global abundance, average latitude across populations, and body mass
 462 as predictors, show that the abundance factor has a significant impact
 463 on population growth. This suggests that weighting species lambda by
 464 global abundance may have biological relevance, as species abundance ap-
 465 pears to positively influence growth potential, consistent with previous
 466 studies on metabolic theory(Brown et al. 2004).

467 4.2 Limitation and Future Work

468 During data preparation, I calculated the I value sequence for each species
 469 based on the selected species lambda dataset. All I value sequences begin
 470 at 1 and reflect the overall trends in species abundance over time. So the
 471 robust calculation of weighted LPI could also be achieved theoretically
 472 via calculating I value sequence of each species firstly and then getting
 473 weighted average of different species I values by global abundance. How-
 474 ever, many species have null lambda values in the initial years, making it
 475 difficult to calculate I value sequences for numerous species. So future
 476 LPI research should focus on analyzing time sequences of population

abundance in the Living Planet dataset using machine learning. This could involve referencing various variables in the LPD, such as populations' latitude data, to develop suitable Convolutional Neural Network (CNN) models for training original LPD and predicting null values in each population's abundance sequence.

4.3 Adjustment for LPI

The basic LPI calculation is based on one of the most extensive time series databases concerning vertebrate populations(Collen et al. 2009). In terms of my research, each abundance sequence I have obtained is considered as a combined population of global populations for each corresponding species because the species lambda sequences obtained via the rlpi package represent averaged growth rates series of all populations of each species, and the 9700 birds' abundance data covers a global scale as well(Tuomisto 2010). Therefore, the LPI calculation in my research is conducted at the level of species' global populations, rather than individual populations.

In previous studies, weighted averaging was also used in the calculation of original LPI, but not weighted via abundance. In the calculation of the average species lambda of each realm, the lambda time series of different species were firstly grouped by class, and then the data at each time point in each class group were averaged to obtain the average lambda time sequence of each class. After that, the lambda time sequences of all classes were weighted and averaged by the actual number of species in each class to obtain the weighted lambda time series by species numbers of each realm(McRae et al. 2017). The numbers of species in different classes serve as the contributions of species' growth in each class to the development of each realm. Given the scope of my research, the LPI study is only about aves because I matched species lambda dataset with global abundance dataset of 9,700 bird species. Even if taxonomic order were used as a lower-level classification standard, the original LPI weighting process would still be unachievable for my work due to the difficulty in obtaining the number of species from different orders within each realm. Secondly, while previous LPI studies fil-

tered population abundance sequences to represent global populations, the resulting datasets still largely reflected abundance changes across most species within each class. In order to get robust data for calculating species global abundance time sequences, my dataset was reduced to only 304 species after multiple filtering steps. Data of selected 304 species is insufficient to represent overall biomass changes in global scale but could serves as more robust data foundation when calculating weighted LPI by abundance according to the hypothesis about abundance's influence on species' growth. Moreover, the weighted LPI by abundance in my research resolved the problem that there is no comparability between abundance time sequences of different species.

4.4 Adjustment for Hill number

In the process of estimating global abundance sequences, the time when the global abundance was selected is without the time range of species lambda dataset, so there is bias between the global abundance sequences I obtained and the actual abundance data. Although the species abundance dataset derived from data scaling may not strictly serve as perfect resource for original Hill number analysis, the trend of abundance sequences and abundance's magnitude are correct because I value sequences are results of cumulative calculation, which could simulate the growth of species abundance. On the other hand, the calculation process for the Hill number in this research does account for relative abundance. Relative abundance can serve as a measure of species' influence (James & Rathbun 1981), which can be adjusted by modifying the q values in the Hill number calculation (Chao et al. 2014). Therefore, although it is not the original Hill number, it remains a reliable metric for reflecting changes in species biodiversity.

4.5 Living Planet Indexes

In all species group, dominant species group and rare species group, there are remarkable differences between the original LPI and weighted LPI by abundance. There are more negative values in growth rate sequences of weighted LPIS than original ones in these mentioned groups. These

542 results demonstrate that in groups with lower species evenness level or
543 sensitivity, the weighting process by abundance could make significant
544 difference in LPI values.

545 Previous research shows that when a community is primarily composed
546 of dominant species, the level of evenness tends to stabilize because the
547 influence of rare species on evenness is minimal and the dominant species'
548 abundance is stable (Chao & Ricotta 2019). In such cases, the develop-
549 ment of the community is reflected on changes in other factors of biodi-
550 versity such as biomass rather than species diversity. As a result, trends
551 of both original and abundance-weighted LPIs differ significantly from
552 the Hill number trend in dominant species groups. Research indicates
553 that genetic diversity and species diversity interact to affect biomass
554 (Crawford & Rudgers 2012). As a result, the weighted LPI by abundance
555 should be used to track biodiversity changes over time in communities
556 with dominant species, as it encompasses multiple aspects of biodiversity,
557 including genetic diversity.

558 **4.6 Hill numbers**

559 In my research, species richness within each abundance-based species
560 group remained stable at most time points. Changes in the Hill num-
561 ber were primarily driven by fluctuations in species evenness, as no ex-
562 tinctions were observed according to the species lambda dataset. Con-
563 sequently, as the q value increases, the fluctuations in sequences become
564 more pronounced, varying in magnitude across different abundance-based
565 species groups due to the increased weighting of evenness and the differ-
566 ing sensitivities of these groups to evenness. The Hill number sequences
567 across different abundance-based groups do not follow the inverse trend
568 of the sequence of standard deviations of the abundance distribution. It
569 means that the trend of species evenness indicated by Hill number is dif-
570 ferent from the trend shown by abundance distribution. Changes in Hill
571 number sequences are particularly acute in the middle abundance and
572 less rare species groups compared to others. Thus, it is the combined
573 effect of both abundance distribution and other factors including even-
574 ness sensitivity that leads to the varying growth rates of Hill number se-

575 sequences across different abundance-based species groups at different time
576 points.

577 **4.7 Pielou evenness and $Ip(\lambda)$**

578 Pielou's evenness is typically considered a reliable index of evenness be-
579 cause it is less affected by species richness (Gosselin 2006). However, in
580 my research, its changing rates consistently remained low, indicating that
581 the stability in Pielou's evenness may be largely influenced by the un-
582 changed species richness. Therefore, I did not pursue further analysis on
583 it.

584 Generalized levels of relative evenness expressed by $Ip(\lambda)$ in different
585 abundance-based species groups are similar to different groups' Pielou
586 evenness levels while development trends of $Ip(\lambda)$ indexes are similar to
587 those of Hill numbers($q=2$). So my research illustrates that $Ip(\lambda)$ could
588 indicate relative evenness to large extend.

589 **4.8 Evenness Sensitivity Analysis**

590 In my research, I measured the sensitivity of different abundance-based
591 species groups to evenness by analyzing how the growth rates of Hill
592 number sequences changed as the q value increased. The reason why I
593 chose this measurement is that these changes in growth rates were more
594 significant than those observed in $Ip(\lambda)$ sequences when the λ value var-
595 ied and changes in Hill numbers while q value changes are not effected by
596 species richness due to its unchanged level.

597 According to the GLM fitting results, P-values of coefficient for abun-
598 dance distribution could reach significant level within abundance-based
599 species groups that have lower standard deviations in abundance distri-
600 bution. This suggests that though the evenness measurements typically
601 consider other aspects of species diversity (Blowes et al. 2022), in cases
602 where abundance distribution is highly even and could cause extremely
603 more significant effect on relative evenness than other coefficients, it is
604 possible to represent species evenness by abundance distribution. Be-
605 cause in that case, abundance distribution is the most dominant factor
606 of relative evenness. The p-values of both coefficients are less than 0.05

607 in all species group and rare species group, not reaching significant level.
608 It shows that in these cases, species evenness has weak connections with
609 both abundance distribution and sensitivity to evenness. So species even-
610 ness do have connections with other factors of biodiversity in ecological
611 aspect Moreover, further research on evenness sensitivity is needed to ex-
612 plore additional dimensions of species evenness as coefficients of evenness
613 sensitivity are not significant in most abundance-based species groups
614 except for rare species group.

615 **4.9 Broader Implications and Future Directions**

616 Species diversity is a priority in biodiversity policy across many contexts
617 (Henle et al. 2013). Evenness sensitivity may link other biodiversity fac-
618 tors to species evenness and serve as a valuable indicator for biodiversity
619 policymakers, as it helps identify the primary drivers of species evenness
620 to some extent. If the coefficient of evenness sensitivity is much more
621 significant than that of abundance distribution in the GLM, the com-
622 munity's relative evenness is mainly influenced by evenness sensitivity,
623 then efforts to adjust evenness levels should focus on other aspects of
624 the community's biodiversity to adjust community's sensitivity to even-
625 ness rather than its abundance distribution. More robust models need
626 to be developed in the future to analyze different dimensions of species
627 evenness, allowing the fitting results to identify the main factors of even-
628 ness through p-values. However, the methodology for calculating even-
629 ness sensitivity should be adapted to the community's status. In cases
630 where species richness fluctuates significantly, the growth rate changes of
631 $Ip(\lambda)$ sequences when λ values change should be referred to as a factor
632 of community's sensitivity to evenness because the calculation of $Ip(\lambda)$ is
633 independent from species richness. Additionally, further analysis on more
634 dimensions of species evenness is needed to develop a robust indicator of
635 evenness sensitivity, as its p-values do not reach the significant level in
636 several abundance-based species groups in my research.

⁶³⁷ 5 Data and Code Availability

⁶³⁸ The Living Planet Dataset (LPD), foundational for all analyses, can be
⁶³⁹ downloaded from <https://www.livingplanetindex.org>. The global
⁶⁴⁰ species lambda dataset, derived from the LPD, is accessible via the `rmpi`
⁶⁴¹ R package at [https://github.com/Zoological-Society-of-London/](https://github.com/Zoological-Society-of-London/rmpi)
⁶⁴² `rmpi`. The dataset on birds' body mass can be downloaded from <https://academic.oup.com/biolinnean/article/163/data>. The LPI com-
⁶⁴³ pleteness data, indicating the percentage of each population in the LPD
⁶⁴⁴ that represents the global populations of the corresponding species, is yet
⁶⁴⁵ to be formally published. The results of the datasets collated in this re-
⁶⁴⁶ search can be found in this repositories: https://github.com/Zhin-Xu/Fanshu_Research_Project2.

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