Running Head: Abundance-Occupancy Relationships

Inter-specific Variability in Demographic Processes Affects Abundance-Occupancy Relationships

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Abstract

Species with large local abundances tend to occupy more sites. One of the mechanisms proposed to explain this widely reported inter-specific relationship is a cross-scale hypothesis based on dynamics at the population level. Called the vital rates mechanism, it uses within-population demographic processes of population growth and density dependence to explain how positive inter-specific abundance-occupancy relationships can arise. Even though the vital rates mechanism is mathematically simple, it has never been tested directly because of the difficulty in estimating the demographic parameters involved. Here, using a recently introduced mark-recapture analysis method on 17 bird species, we show that inter-specific variability in density dependence strength can weaken both abundance-occupancy relationships and the expected corollaries of the vital rates mechanism. We demonstrate that one of the key assumptions of vital rates mechanism, that density dependence strength should be similar among species, is not met for these 17 species. Additionally, the mathematical structure of vital rates mechanism that relate population-level abundance and intrinsic growth rate is only weakly observed in our data. We argue that this mismatch of mathematical structure and data together with the violation of density dependence assumption weakens the expected positive abundance-occupancy association. Vital rates mechanism also predicts conditions under which positive abundance-occupancy association is weakened or even reversed; our results are consistent with these predictions. More generally, our findings support a cross-scale mechanism of macroecological abundance-occupancy relationship emerging from density-dependent dynamics at the population level.

Keywords: Abundance, occupancy, density dependence, population demography, intrinsic growth rate, mark-recapture, macroecological patterns

Introduction

Exploring ecological processes and interactions across scales of biological organization allows a deeper understanding of patterns of biodiversity. One well-documented macro-ecological pattern is the abundance-occupancy relationship: across phylogenetically similar species, local average abundance and proportion of sites occupied are positively correlated (Hanski, 1982; Bock & Ricklefs, 1983; Brown, 1984, 1995; Gaston & Blackburn, 2000). This pattern has been observed in a variety of taxa, such as mammals (Blackburn *et al.*, 1997), birds (Lacy & Bock, 1986; Blackburn *et al.*, 1997), butterflies (Conrad *et al.*, 2001), mollusks (Russell & Lindberg, 1988), and plants (Guo *et al.*, 2000). A meta-analysis on abundance-occupancy relationships found strong positive effect size but also reported high variability across species realms (Blackburn *et al.*, 2006). Some species groups, however, show zero or negative correlation between abundance and occupancy (Novosolov *et al.*, 2017), which may be because of an ecological mechanism (Reif *et al.*, 2006; Symonds & Johnson, 2006; Ferenc *et al.*, 2016; Freeman, 2019), or a result of the metrics used to represent abundance and occupancy (Wilson, 2008).

Several mechanisms have been proposed to explain the positive relationship between abundance and occupancy (reviewed by Gaston *et al.*, 1997 and Borregaard & Rahbek, 2010). Among these, one mechanism, known as "vital rates" is notable for being the only one that explains this macro-ecological relationship based on the population dynamics of the species that display the pattern. While explaining the vital rates mechanism, Holt *et al.*, (1997) argued that the positive correlation between number of occupied sites and local average abundance across species is a consequence of the relationship between population abundance and intrinsic population growth rate (r). Species exist only in sites with $r > 0$, and higher r leads to higher

abundances. If r is determined by an environmental gradient, any environmental factor that increases r will also increase abundance at each site and simultaneously increase the number of occupied sites across the same environmental gradient. Differences in intrinsic growth rates among species will lead to the observed positive inter-specific relationship between abundance and occupancy. Using logistic equation, Holt *et al.*, (1997) summarizes the relationship between population abundance and intrinsic growth rate in a temporally variable environment as follows (with slight modifications for clarity):

$$\bar{N}_{i,k} = \frac{\bar{r}_{i,k}}{\mu} \qquad Eq.\ 1$$

where $\bar{N}_{i,k}$ is the long-term average abundance of population k of species i; $\bar{r}_{i,k}$ is the long-term intrinsic growth rate; and μ is density dependence strength. This relationship between population abundance and intrinsic growth rate leads to positive abundance-occupancy relationships across species, if four major assumptions are correct: 1) Response curves of r vs. environmental factors are similar across species; 2) Environmental factors are uniformly and continuously distributed across landscape, creating a smooth gradient; 3) Density dependence is similar across species; 4) Dispersal rates are not high enough for continuous existence of a large number of sink populations.

Although the vital rates mechanism is one of the simplest explanations for positive abundance-occupancy relationships (Gaston *et al.*, 1997), it has been empirically tested only a few times because of the difficulty of estimating the demographic parameters involved. For example, Freckleton *et al.*, (2006) relaxed the second assumption indicated above and showed how abundance-occupancy relationship changes depending on the distribution of habitat suitability and its effect on death rates (but ultimately on r). The statistics they derived (e.g., left or right skewness in population size) was consistent between real data and analytical

expectations from the vital rates mechanism. Similarly, Freckleton *et al.*, (2005) relaxed the fourth assumption and investigated the effects of colonization dynamics on the abundance-distribution patterns. While these studies contributed to our understanding of the dynamics behind vital rates mechanism, they did not estimate relevant demographic parameters from real data (for example, r and density dependence strength), which is essential to test this hypothesis because it is ultimately a mechanism about the demography of populations.

Here, we use a recently introduced modelling framework, called CJS-pop (Şen & Akçakaya, 2020) to estimate the vital rates of 17 bird species and explicitly test the assumptions and predictions of Holt *et al.*, (1997)'s vital rates mechanism. CJS-pop employs robust-design mark recapture data and can estimate survival, fecundity, and density dependence of vital rates. CJS-pop can also model vital rates (here, survival and fecundity) as functions of environmental factors. Survival and fecundity can be used to derive the intrinsic growth rate of a population by setting population density to zero, in which case growth rate will only vary along the gradient of environmental factors used in CJS-pop. Accordingly, CJS-pop framework can be used to estimate the necessary demographic parameters for testing the vital rates mechanism: a spatially variable and environmentally determined intrinsic growth rate, density dependence strength of vital rates, population size and metrics of occupancy.

We tested the vital rates mechanism of Holt *et al.*, (1997) by answering the following questions about the demographic processes and patterns within and among species that form the basis of their hypothesis.

1. *Is there a positive correlation between local abundance and occupancy among species?* This is the primary macroecological pattern that the vital rates hypothesis explains. We investigate, using three different occupancy metrics, if there is an inter-specific relationship

between abundance and occupancy among 17 bird species (see sections below for details on species selection)

2. *Is there a positive correlation between abundance and intrinsic growth rate among populations within species?*

Logistic equation can be expressed in a form in which average abundance of a population is directly proportional to average intrinsic growth rate and density dependence strength (Eq. 1; Holt *et al.*, 1997). CJS-pop does not force this relationship on estimates of demographic parameters, so it can be used to independently test whether this pattern is observed in the data. For each species, we estimate an overall (not population-specific) strength of density-dependence, so this relationship can be simplified to a correlation between population-level abundance and intrinsic growth rate of a species.

3. *Is there a correlation between abundance and intrinsic growth rate among species?*

An important corollary of Eq. 1 is that species-level average intrinsic growth rate and local average abundance should be positively correlated across species. This follows the fact that population level abundance and intrinsic growth rate is correlated and species that has more populations with high abundance should also have more populations with high intrinsic growth rate leading to a high average abundance and high average intrinsic growth rate across their populations.

4. *Is there a positive correlation between intrinsic growth rate and occupancy among species?*

Following the previous corollary, if there is a correlation between species-level intrinsic growth rate and abundance, and if abundance is correlated with occupancy, it is expected that intrinsic growth rate should also be correlated with occupancy.

The answers to these questions depend heavily on the assumptions of the similarity of density dependence, and the similarity of response to environmental gradients, among species. Here, we mainly focus on density dependence strength and how it, together with other demographic parameters, can affect macroecological patterns.

Materials and Methods

Data: Mapping Avian Productivity and Survivorship (MAPS)

MAPS is a collaborative mark-recapture program initiated and organized by the Institute for Bird Populations (IBP) since 1989 across 1200 banding stations in US and Canada. The program provides data for more than 300 species. We MAPS data to captures from conterminous United States and from 1992 to 2008 between May and August (breeding season). We considered first year individuals (MAPS age code 2 and 4) as juveniles, and all older individuals (MAPS age code 1,5,6,7, and 8) as adults. Following Albert *et al.* (2016) we only used species with:

1) More than 74 adult individuals, and more than 74 juvenile individuals captured,
2) More than 14 adults, and more than 14 juveniles re-captured.

These filters reduced the dataset to 62 species. We applied CJS-pop to only 42 species which had reasonable data size (e.g. maximum model convergence time was one week). For each species, we treated separate MAPS locations (a cluster of mist-netting and banding stations) to be independent breeding populations. We only included data from populations which have been monitored for at least 5 years.

CJS-pop

CJS-pop uses robust design mark-recapture data as a single data source for parameterizing demographic models in a Bayesian hierarchical framework (Şen & Akçakaya, 2020; also see

Appendix S2 for a detailed explanation of CJS-pop). It can estimate population vital rates (survival and fecundity) as well as density-dependence and process variance in these vital rates (temporal or spatial variability). Here, we model survival and fecundity as functions of environmental covariates in addition to density dependence. An example model structure, here illustrated for $\phi_{x,k,t}$, the survival probability of a stage x invidiual, at population k, and at year t, with two environmental covariates is given as:

$$\text{logit}(\phi_{x,k,t}) = \alpha_x - \beta_1 \cdot D_{k,t} + \beta_2 \cdot W_{1,k,t} + \beta_3 \cdot W_{2,k,t} + \epsilon_t \qquad Eq.\ 2a$$

$$\epsilon_t \sim Normal(0, \sigma_s^2) \qquad Eq.\ 2b$$

where α_x is the survival probability of a stage x individual in logit scale at mean population size and at mean of environmental covariates W_1 and W_2; β_1 is the change in survival in logit scale with one unit change in population density index; D is the population density index at population k, and at year t (See appendix S2 for density index calculation); β_2 and β_3 are the change in survival in logit scale with one unit change in W_1 and W_2, respectively; ϵ_t is the temporal random effect at year t, and σ_s^2 is the temporal process variance of survival at logit scale; $x = 1,2,\ldots,X$; $k = 1,2,3\ldots,K$; $t = 1,2,3\ldots,T$. We denote $x = 1$ as juveniles and, $x = 2$ as adults.

Similarly, fecundity $F_{k,t}$ at population k and year t can be modelled as:

$$\log(F_{k,t}) = \theta - \zeta_1 \cdot D_{k,(t-1)} + \zeta_2 \cdot W_{1,k,t} + \zeta_3 \cdot W_{2,k,t} + \omega_t \qquad Eq.3a$$

$$\omega_t \sim Normal(0, \sigma_f^2) \qquad Eq.3b$$

where θ is the average fecundity in log scale at mean population size and at mean of environmental covariates W_1 and W_2; ζ_1 is the change in fecundity in log scale with one unit change in population density index; ζ_2 and ζ_3 are the changes in fecundity in log scale with one unit change in W_1 and W_2, respectively; ω_t is the temporal random effect at year t, and σ_f^2 is the temporal process variance of fecundity in log scale.

Because CJS-pop is an extended version of a typical Cormack-Jolly-Seber (CJS) method (Şen & Akçakaya, 2020), capture probability $p_{x,k,t,h}$ of a stage x individual at population k, year t, and month h is explicitly modelled alongside vital rates as a function of capture effort:

$$\text{logit}(p_{x,k,t,h}) = \gamma_x + \delta \cdot E_{k,t,h} \qquad Eq.4$$

where γ_x is the monthly capture probability on logit scale of a stage x individual at mean capture effort; δ is the change in monthly capture probability on logit scale with one unit change in capture effort; E is the capture effort, which is calculated as total mist netting hours per month in a population; $h = 1,2,3\ldots,H$.

Environmental Covariates

We used the downscaled Maurer gridded data (Maurer et al., 2012), which was shown to be superior to several other alternatives in terms of its closeness to observed measurements (Behnke *et al.*, 2016), to calculate the ten metrics used as environmental covariates in CJS-pop models: annual mean temperature, mean diurnal range, mean temperature of wettest quarter, annual precipitation, precipitation of Warmest Quarter, maximum consecutive dry days, maximum consecutive 5-day precipitation total for March, standard deviation in daily temperatures for March, total precipitation in May, and number of dry days in April. We used annual aggregates of these metrics when building CJS-pop models. Each MAPS location was assigned the covariate values of the grid cell it was located in. If the mist-netting stations of a location was distributed across multiple grid cells we assigned the average value of the covariates across those grid cells to that location. We repeated this process for every year between 1992-2008 for every MAPS location, creating a time series of weather variables at each location.

To prevent overfitting and fasten the convergence of CJS-pop, we reduced the number of covariates with principal component analysis (PCA) and used the number of principle components that cumulatively explains 80% of the variation. We applied PCA separately to each species using the time series of weather covariates from the MAPS locations a given species was captured in.

Estimating Demographic Parameters

Intrinsic Growth Rate

Intrinsic population growth rate is the density independent population growth rate. While the exact meaning depends on the estimation method (Lynch & Fagan, 2009), it represents the theoretical maximum of a population's ability to grow in size when population density is close to 0. To estimate intrinsic growth rate at a given population and year, we set density to 0 and estimate survival and fecundity only as functions of environmental covariates. We use posterior means of parameters, as estimated by CJS-pop, and omit process variance when estimating survival and fecundity. Then, separately for each species, intrinsic growth rate $r_{k,t}$ at population k and year t can be estimated as:

$$r_{k,t} = \log\left(\phi'_{2,k,t} + \phi'_{1,k,t} \cdot F'_{k,t}\right) \qquad Eq.5$$

where $\phi'_{2,k,t}$ is the adult survival at population k and year t at 0 density; $\phi'_{1,k,t}$ is juvenile survival at 0 density; and $F'_{k,t}$ is fecundity at 0 density. We estimate average intrinsic growth rate of each population as geometric mean:

$$\overline{r_k} = \sqrt[T]{\prod_{t=1}^{T} r_{k,t}} \qquad Eq.6$$

Finally, to estimate species level intrinsic growth rate we use the median of population level growth rates:

$$\bar{\bar{r}} = \text{median}(\bar{\mathbf{r}}) \qquad Eq.7$$

where, $\bar{\mathbf{r}}$ is a vector with population level intrinsic growth rates.

We only used species with a negative density-dependence effect on growth rate (growth rate at density index 2 was lower than growth rate at density index 0). Intrinsic growth rate is not defined for circumstances in which increasing density also increases the population growth; in such a case intrinsic growth rate loses its meaning as a theoretical maximum. Additionally, positive density dependence effects are biologically meaningful only when Allee effects are considered. Because we are not modelling Allee effects with CJS-pop, we removed species that showed a positive density dependence effect on growth rate from further analysis.

Population Size

The monthly capture probabilities obtained from CJS-pop are used to calculate the yearly capture probabilities, and these in turn are used to estimate the expected size of each population in each year. Yearly capture probabilities for each adult and juvenile in a given year and population is calculated as follows:

$$P_{x,k,t} = 1 - \prod_{h=1}^{4} \left(1 - p_{x,k,t,h}\right) \qquad Eq.8$$

where, $P_{x,k,t}$ is the probability that a stage x individual will be captured at least once in 4 months of the breeding period at year t and population k.

Using the heuristic estimator for population size with a correction for years with 0 captures (Dail & Madsen, 2011), the numbers of adults and juveniles can be derived as:

$$N_{x,k,t} = \frac{n_{x,k,t}}{P_{x,k,t}} + \frac{\left(1 - P_{x,k,t}\right)}{P_{x,k,t}} \qquad Eq.9$$

where, $n_{x,k,t}$ is the number of captured stage x individuals at population k and year t, and $N_{x,k,t}$ is the expected number of stage x individuals of the same population and year combination. Average total population size for each population is estimated as:

$$\overline{N_k} = \frac{\sum_{t=1}^{T} N_{1,k,t} + N_{2,k,t}}{T \cdot m_k} \qquad Eq.10$$

where, T is the number of sampling years of a population. MAPS locations can have different number of stations, we standardize total population size by dividing by the number of stations of population k, m_k. We estimate the species level population abundance as the median population size across all populations:

$$\overline{\overline{N}} = median(\overline{\mathbf{N}}) \qquad Eq.11$$

where, $\overline{\mathbf{N}}$ is a vector with average population sizes.

Occupancy

There are 1019 mist netting stations and 495 MAPS locations across US in the dataset we used for this analysis. The number of mist netting stations and number of MAPS locations a species was captured in provides information about the distribution and occupancy of a species. Different measures of occupancy affect the strength of estimated abundance-occupancy relationship (Borregaard & Rahbek, 2010). Here, we define occupancy using three different measures: 1) geographic extent calculated as 100% minimum convex polygon of all the stations in which a species was captured; 2) number of different populations (MAPS locations) in which a species was captured; and 3) number of different mist-netting stations in which a species was captured.

Testing Hypothesis

We tested macroecological hypotheses using Bayesian statistics. For each hypothesis, we estimate Pearson's correlation coefficient (ρ) and report the posterior probability of the hypothesis, $P(\rho > 0)$. To answer questions stated in the introduction, we estimate ρ and test hypothesis of $P(\rho > 0)$ for the following demographic parameter pairings: $\overline{\overline{N}}$ vs Occupancy, $\overline{r}_k$ vs $\overline{N}_k$, $\overline{\overline{N}}$ vs $\overline{\overline{r}}$, $\overline{\overline{r}}$ vs Occupancy; noting that the second of these pairings is an intra-species relationship, tested for each species separately while the remaining three pertain to inter-specific relationships. Because we use uniform priors on ρ ($\mathrm{Uniform}(-1,1)$), posterior probability estimates above or below 0.5 can be considered as evidence obtained from data regarding the hypothesis being tested. Detailed information on priors and model specifications of all Bayesian models used in this analysis (including CJS-pop) can be found in Appendix S2. R code for data manipulation and JAGS code for the CJS-pop framework are available at https://github.com/bilgecansen/VitalRatesTest. Results of CJS-pop models and data for hypothesis testing is in Data S1.

Results

Species Selection

Of the 42 species analyzed, 34 yielded posterior distributions that converged ($\hat{R} < 1.1$ for all parameters). Of these 34 species, only 17 had an overall negative density dependence effect on growth rate (Table 1). Among these 17 species, population size showed a right skewed distribution with many small and few large populations (Appednix S1: Fig. S1a). The majority of these populations have $\overline{r} > 0$ with unimodal distribution that is centered on 0.14 (Appendix S1: Fig. S1b).

Is there a positive correlation between $\overline{\overline{N}}$ and occupancy?

We found no evidence that $\overline{\overline{N}}$ is correlated with geographic extent ($\rho = 0.012$, $P(\rho > 0) = 0.523$) or with the number of stations ($\rho = 0.056$, $P(\rho > 0) = 0.598$; Figs. 1a and 1e). There is, however, a weakly positive relationship between $\overline{\overline{N}}$ and number of populations ($\rho = 0.261$, $P(\rho > 0) = 0.865$; Fig. 1c).

Is there a positive correlation between $\overline{r}$ and $\overline{N}$ among populations of each species?

There was a positive relationship between $\overline{r}$ and $\overline{N}$ for 13 out of 17 species. The strength and uncertainty of these relationships are highly variable among species (Fig. 2). Seven species have $P(\rho > 0) > 0.9$, indicating strong evidence for the inferred positive relationship between intrinsic growth rate and population size at the population level. Downy Woodpecker has the highest correlation coefficient with the lowest uncertainty ($\rho = 0.42$ $(0.31 - 0.53)$). Wrentit is the only species with a strong negative relationship between $\overline{r}$ and $\overline{N}$ (Fig. 2).

Is there a positive correlation between $\overline{\overline{r}}$ and $\overline{\overline{N}}$?

We found a strong negative correlation between $\overline{\overline{r}}$ and $\overline{\overline{N}}$ ($\rho = -0.513$) indicating a very low probability of a positive relationship ($P(\rho > 0) = 0.017$; Fig. 3).

Is there a positive correlation between $\overline{\overline{r}}$ and occupancy?

We detected a weak and positive relationship between geographic extent and $\overline{\overline{r}}$ ($\rho = 0.126$, $P(\rho > 0) = 0.700$; Fig. 1b). While the signs of estimated ρ are different for $\overline{\overline{r}}$ vs number of populations and $\overline{\overline{r}}$ vs number of stations, they are both close to 0 ($\rho = -0.073$ and 0.099, respectively), and they provide no conclusive evidence for a consistent relationship with $\overline{\overline{r}}$ in either direction ($P(\rho > 0) = 0.346$ and 0.620; Figs. 1d and 1f).

Density Dependence

There is a strong negative correlation between density dependence strength in survival (β) and $\overline{\overline{N}}$, and strong positive correlation between β and $\overline{\overline{r}}$, which indicates that species with small average population size and large intrinsic growth rate are associated with stronger density dependence in survival (Fig.s 4a and 4c). Relationship between density dependence in fecundity (ζ) and $\overline{\overline{N}}$ and $\overline{\overline{r}}$ shows the opposite trend to their survival counter parts, albeit with weaker ρ estimates (Figs. 4b and 4d).

Discussion

The four questions we asked follow the fundamental logic behind Holt *et al.*, (1997)'s vital rates mechanism. First, if there is a positive relationship between abundance and occupancy across species and if that relationship is driven by vital rates mechanism, population-level abundance and intrinsic growth rate should be correlated within a species (Eq. 1). We detected weaker relationships between abundance and different metrics of occupancy (Figs. 1a, 1b, and 1c) when compared to other abundance-occupancy studies on birds (Bock & Ricklefs, 1983; Lacy & Bock, 1986; Hurlbert & White, 2007; Webb *et al.*, 2007). Additionally, only seven species showed a high probability of positive correlation between $\overline{r}$ and $\overline{N}$ among their populations, and the strength of these correlations tend to be weak as well (Fig. 2).

Secondly, as a corollary of vital rates mechanism and its assumption that density dependence strength among species should be similar, species-level growth rate and abundance should also be positively correlated. However, we observe the exactly opposite: a strongly negative relationship between $\overline{\overline{r}}$ and $\overline{\overline{N}}$ (Fig. 3). We argue that the main reason we don't see a positive relationship between $\overline{\overline{r}}$ and $\overline{\overline{N}}$ is the violation of the assumption that the strength of density dependence is similar among species. Variability in the strength of density dependence,

together with the weak relationship between $\bar{r}$ and $\bar{N}$ among populations of each species, prevents a positive abundance occupancy association and results in weak relationships of both $\bar{\bar{r}}$ and $\bar{\bar{N}}$ with occupancy metrics in Fig. 1. If all species have similar density dependence (e.g., in terms of the mechanism, but especially in terms of strength), then species with higher average growth rate will also have higher average abundance and higher occupancy; thus, all three variables would be correlated among species. However, if the strength and other properties of density dependence varies among species, such a pattern would not exist. Holt *et al.*, (1997) predicted that variable density dependence strength among species might break the positive association between abundance and occupancy, writing that "[a] species with small r but weak density dependence can obtain enormous local abundances compared to another species with large r but intense density dependence". We hypothesize that this is exactly the pattern we report here.

Holt *et al.*, (1997) predicted when the relationship between intrinsic growth rate and density dependence should break down positive occupancy-abundance relationships. The relationship between density dependence strength and growth rate (Fig. 4c) is similar to Holt *et al.*, (1997)'s prediction (see their Fig. 4, region C). For the 17 species that we have modeled, the strength of density dependence in survival shows considerable variation among species leading to the relationship in Fig. 4c. It seems likely that this variability is responsible for the weak relationship detected between $\bar{\bar{N}}$, $\bar{\bar{r}}$ and occupancy metrics (Fig. 1). Although we do not know the exact ecological process that lead to these relationships (Fig. 4), there seems to be a pattern to the trade-off among growth rate, average abundance, and density dependence across species. Species with lower growth rate have higher abundance and are strongly regulated by density dependent processes, especially acting on survival rates. Species with higher growth rate, on average, have

lower abundance and are more weakly regulated by density dependent processes especially acting on fecundity. We are not aware of any other study exploring these patterns, so a better understanding of the relationship of density dependence with other demographic parameters and the macroecological patterns they might cause requires further research of these patterns in other taxonomic groups.

The correlation between $\bar{r}$ and $\bar{N}$ among populations of a species is the mathematical foundation of the vital rates mechanism. The structure of this version of logistic equation implies perfect correlation (assuming that density dependence strength is a species-specific trait and therefore constant across populations of the species). To explore whether such strong correlations exist among populations, a model should allow $\bar{r}$ and $\bar{N}$ to vary independently. CJS-pop is one such modelling framework in which any kind of relationship between $\bar{r}$ and $\bar{N}$ can naturally arise. The majority of the 17 bird species considered show positive correlation between $\bar{r}$ and $\bar{N}$ among their populations, but these correlations tend to be weak (Fig. 2). We argue there is more nuance to this relationship between $\bar{r}$ and $\bar{N}$, and their correlation should not be assumed by default. These weak correlations likely play a role in weakening and sometimes reversing the positive abundance-occupancy relationships observed in Fig. 1. A weak correlation between $\bar{r}$ and $\bar{N}$ can also indicate a spatially varying density dependence strength among the populations of a species. This would mean that both resource availability and the response of a population to available resources varies across populations for a given species. This mechanism is also hypothesized to prevent positive abundance-occupancy relationships (Holt *et al.*, 1997). While CJS-pop can be modified to fit a population specific density dependence strength, none of the species have enough data to provide such information. We believe this is an exciting future research topic.

Density dependent dynamics, of course, are not the only factors that can explain weak or negative abundance-occupancy relationships. Below we explore if other ecological processes can lead to the patterns we report here. For a discussion on how statistical artefacts can affect the patterns we report here see Appendix S2.

Alternative Processes to Density Dependence

An alternative mechanism that may cause a weak relationship between abundance and occupancy is local adaptation in range-restricted species. For example, adaptation of mountainous bird species to their local environments, especially in the afro-tropical region, has been hypothesized to break down the correlation between range size and abundance (Reif *et al.*, 2006; Symonds & Johnson, 2006; Ferenc *et al.*, 2016; Freeman, 2019). These mountainous species are highly adapted to high elevation areas and can reach abundance levels similar to lower elevation species while still occurring across a narrower range. Although this mechanism can explain the lack of a positive abundance occupancy relationship of specialist species with a narrow range, it is not applicable to our study because majority of the17 bird species we modeled are wide-ranging across US.

Another important mechanism that can affect the abundance-occupancy relationships is dispersal and colonization-extinction dynamics. Individuals of the species we have modeled are rarely captured in multiple populations (MAPS locations), so we cannot estimate dispersal rate from the data we are using and at the scale we are applying CJS-pop. A future goal is to use multiple data sets, one for species movement and another for species demography, to explore how their interaction can affect abundance-occupancy relationships.

In addition to similarity of density-dependence strength across species, one of the most important assumptions of the vital rates mechanism is that species should show a similar

response to an environmental gradient in terms of how their vital rates are affected. Variable responses can explain the patterns we observed. Here, this response is quantified in the slopes estimated by CJS-pop for environmental variables. There are two complications for comparing these slopes:

1) Because we use the principal component dimensions of environmental variables as covariates in CJS-pop, the fitted slopes do not represent the response to same environmental variables. Each dimension of each species will be different from others.
2) The response to an environmental gradient that is described by Holt *et al.*, (1997) is more akin to the concept of fundamental niche. CJS-pop, or any other statistical method, may not be able to estimate the "true" response to environmental variability for the simple fact that species may not occur in every suitable site because of competitive exclusion. Inter-species biotic interactions are effectively missing from the vital rates mechanism.

Patterns of distribution of life on Earth are interesting in themselves, but even more so when they are associated with, and explained by, mechanisms at different levels of biological organization. Holt *et al.*, (1997) presented one such mechanism for the widely reported positive abundance-occupancy relationships. It is, however, likely that the abundance-occupancy patterns are simultaneously determined by dispersal, inter-specific and intra-specific interactions, species demography and response to environmental gradients, as well as the sampling schemes used to explore these relationships. Here, we only demonstrated the effect of within-population processes. Ideally, macroecological patterns would be explored in frameworks that include dynamics at all relevant scales, including processes that are at the population, metapopulation,

and assemblage or community levels, and different sampling schemes. Such cross-scale frameworks would help us get a clearer picture of the conditions under which abundance-occupancy and other macroecological relationships emerge.

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Table 1. Names of the17 selected species to be used in testing the vital rates mechanism.

4-Letter Code	English Name	Scientific Name
ACFL	Acadian Flycatcher	Empidonax virescens
BRCR	Brown Creeper	Certhia americana
CACH	Carolina Chickadee	Poecile carolinensis
CALT	California Towhee	Melozone crissalis
DOWO	Downy Woodpecker	Dryobates pubescens
HAWO	Hairy Woodpecker	Dryobates villosus
HUVI	Hutton's Vireo	Vireo huttoni
INBU	Indigo Bunting	Passerina cyanea
LISP	Lincoln's Sparrow	Melospiza lincolnii
MOCH	Mountain Chickadee	Poecile gambeli
RCSP	Rufous-crowned Sparrow	Aimophila ruficeps
REVI	Red-eyed Vireo	Vireo olivaceus
SPTO	Spotted Towhee	Pipilo maculatus
TUTI	Tufted Titmouse	Baeolophus bicolor
WEWP	Western Wood-Pewee	Contopus sordidulus
WREN	Wrentit	Chamaea fasciata
YBCH	Yellow-breasted Chat	Icteria virens

Figure Legends

Figure 1. Correlations between species level median abundance ($\bar{\bar{N}}$), median intrinsic growth rate ($\bar{\bar{r}}$) and metrics of occupancy. The orange is the best fit OLS line to indicate the trend in the data. ρ is the Pearson's correlation coefficient and its 95% credible interval is in parenthesis. $P(\rho > 0)$ indicates the probability that there is positive correlation between two variables.

Figure 2. Correlation between population level abundance ($\bar{N}$) and intrinsic growth rate ($\bar{r}$) for each species. The orange dot indicates the mean of the posterior distribution of Pearson's correlation coefficient (ρ). Black lines are the 50% credible intervals and gray lines are 90% credible intervals of the posterior distributions.

Figure 3. Correlation between species level median abundance ($\bar{\bar{N}}$), median intrinsic growth rate ($\bar{\bar{r}}$). The orange is the best fit OLS line to indicate the trend in the data. ρ is Pearson's correlation coefficient and its 95% credible interval is in parenthesis. $P(\rho > 0)$ indicates the probability that there is positive correlation between two variables.

Figure 4. Correlations between density dependence strength in survival (β), density dependence strength in fecundity (ζ), species level median abundance ($\bar{\bar{N}}$), and median intrinsic growth rate ($\bar{\bar{r}}$). The orange is the best fit OLS line to indicate the trend in the data. ρ is Pearson's correlation coefficient and its 95% credible interval is in parenthesis.

Figure 1

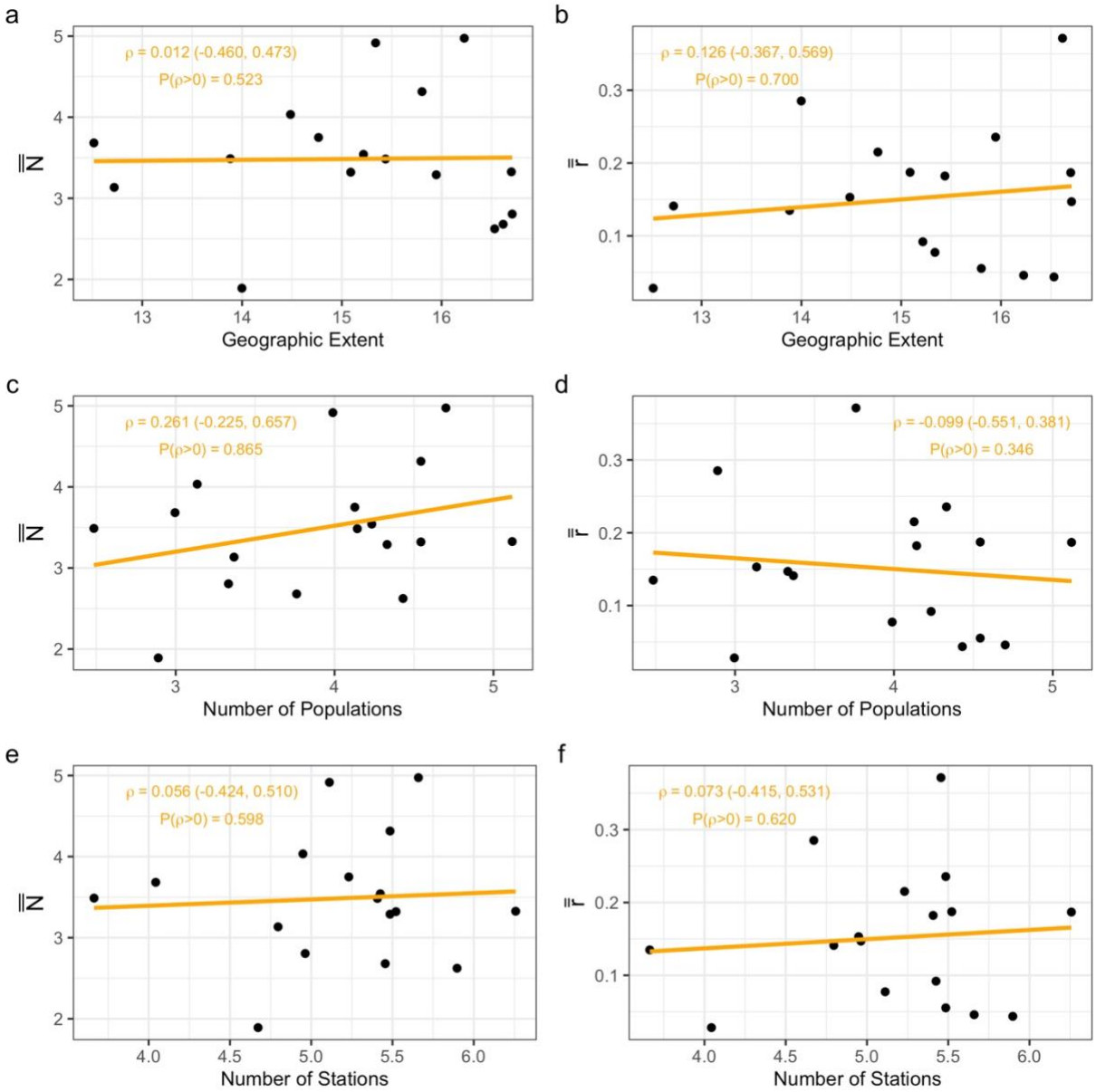

a
ρ = 0.012 (-0.460, 0.473)
P(ρ>0) = 0.523
N̄
Geographic Extent
b
ρ = 0.126 (-0.367, 0.569)
P(ρ>0) = 0.700
r̄
Geographic Extent
c
ρ = 0.261 (-0.225, 0.657)
P(ρ>0) = 0.865
N̄
Number of Populations
d
ρ = -0.099 (-0.551, 0.381)
P(ρ>0) = 0.346
r̄
Number of Populations
e
ρ = 0.056 (-0.424, 0.510)
P(ρ>0) = 0.598
N̄
Number of Stations
f
ρ = 0.073 (-0.415, 0.531)
P(ρ>0) = 0.620
r̄
Number of Stations

Figure 2

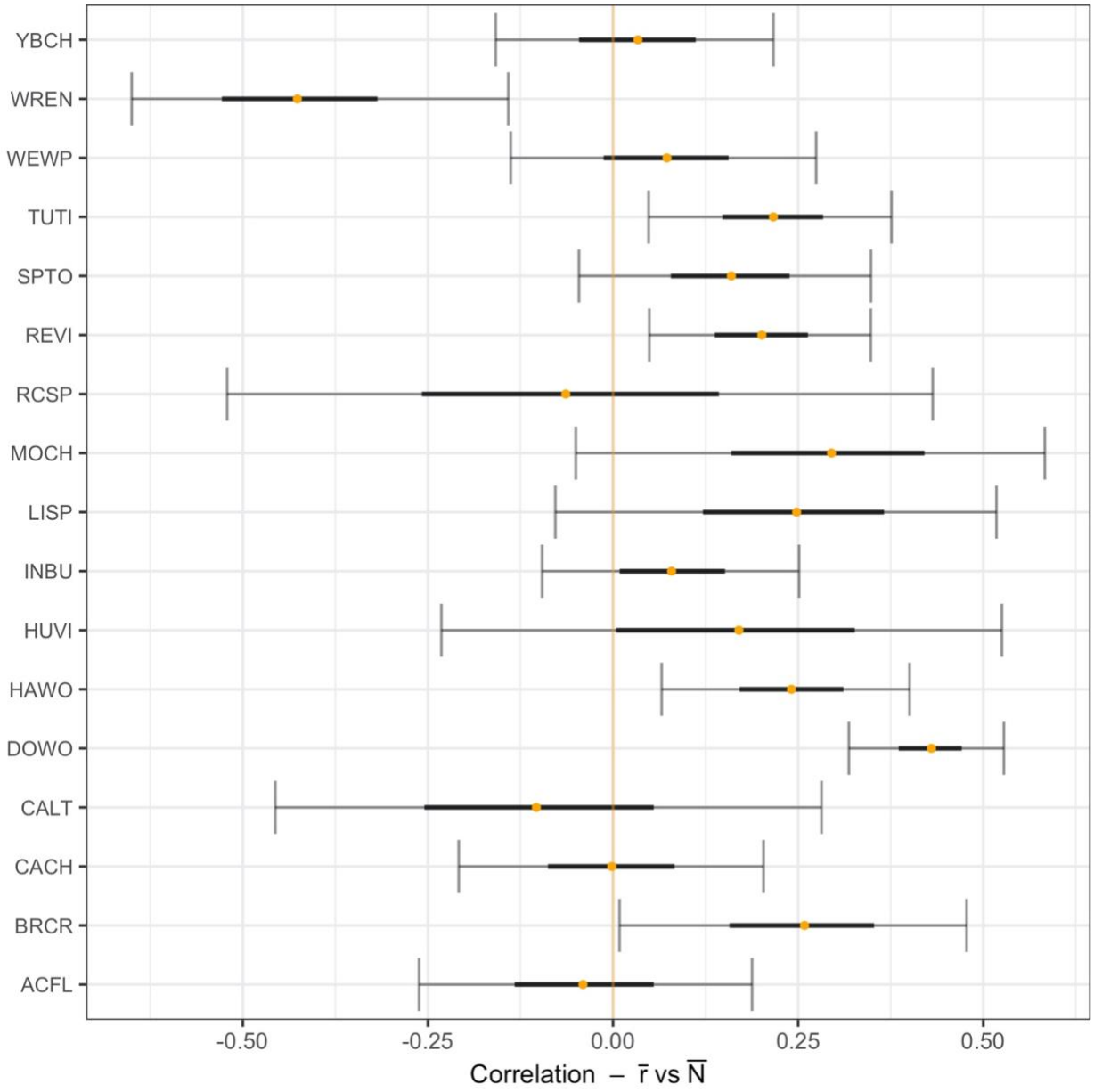

YBCH
WREN
WEWP
TUTI
SPTO
REVI
RCSP
MOCH
LISP
INBU
HUVI
HAWO
DOWO
CALT
CACH
BRCR
ACFL
-0.50
-0.25
0.00
0.25
0.50
Correlation – r̄ vs N̄

Figure 3

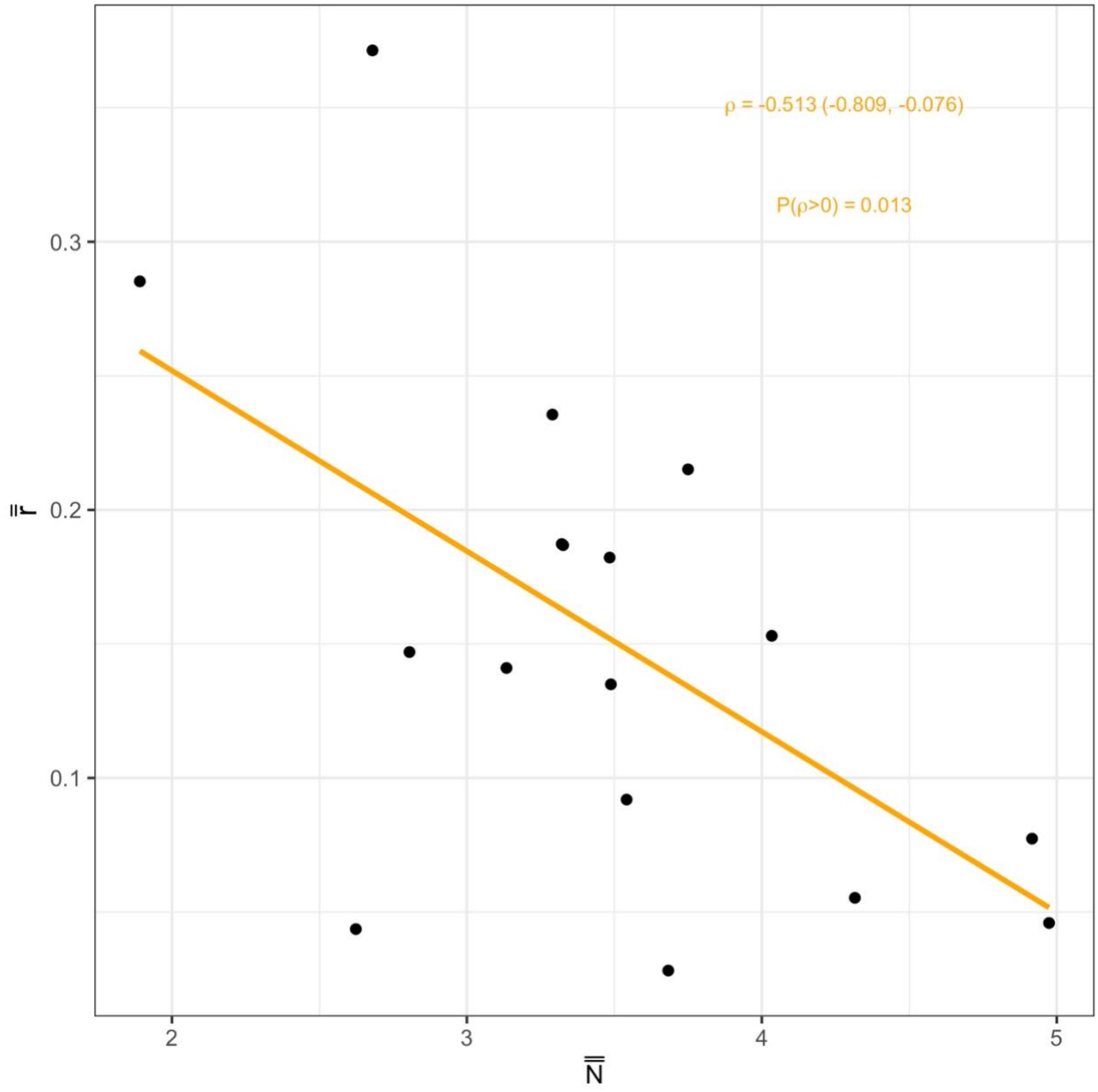
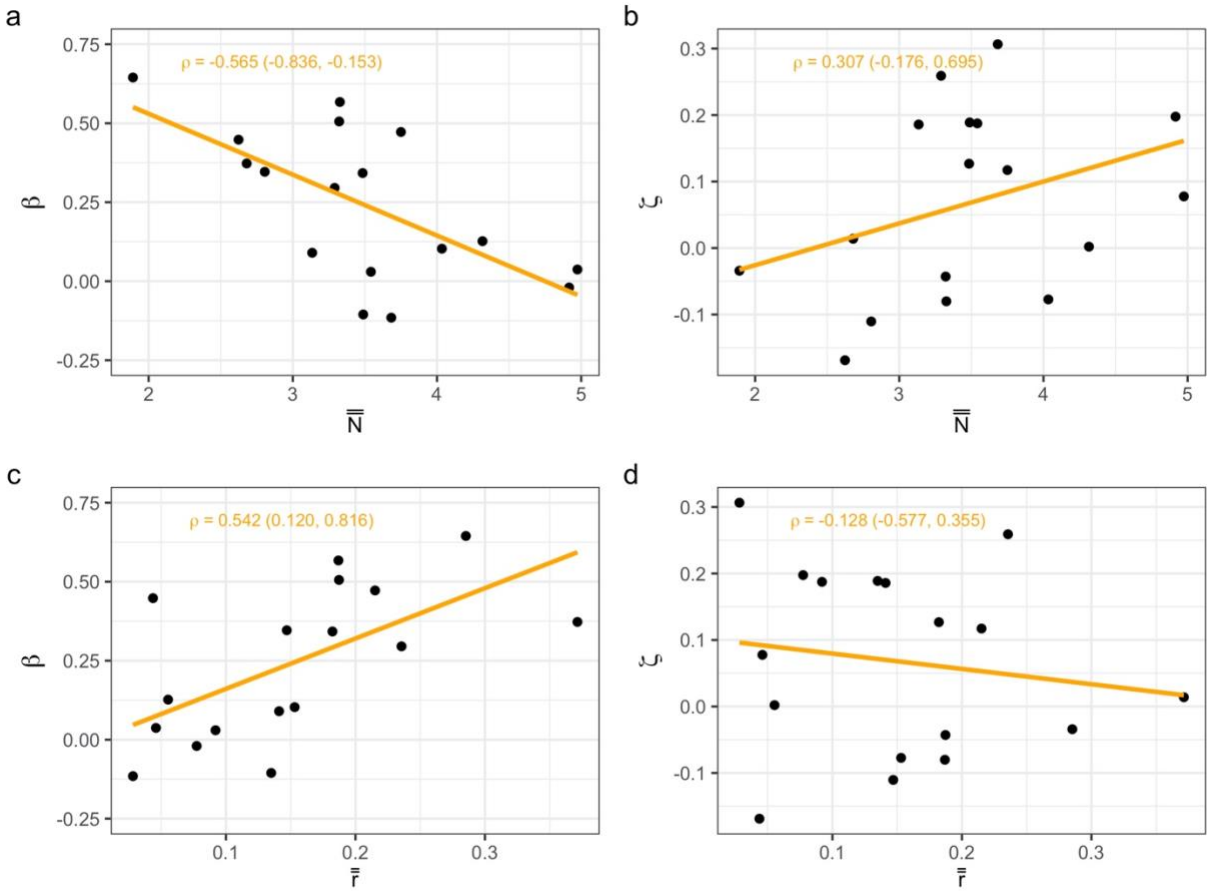


Figure 4


a
ρ = -0.565 (-0.836, -0.153)
β
N̿
b
ρ = 0.307 (-0.176, 0.695)
ζ
N̿
c
ρ = 0.542 (0.120, 0.816)
β
r̿
d
ρ = -0.128 (-0.577, 0.355)
ζ
r̿