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ARTICLE

Functional traits and environment jointly determine the spatial scaling of population stability in North American birds

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Abstract

Understanding the spatial scaling of population stability is critical for informing conservation strategies. A recently proposed metric for quantifying how population stability varies across scales is the invariability–area relationship (IAR), but the underlying drivers shaping IARs remain unclear. Using 15-year records of 249 bird species in 1035 survey transects in North America, we derived the IAR for each species by calculating population temporal invariability at different spatial scales (i.e., number of routes) and investigated how species IARs were influenced by functional traits and environmental factors. We found that species with faster life history traits and reduced flight efficiency had higher IAR intercepts (i.e., locally more stable), whereas migratory species exhibited higher IAR slopes (i.e., a faster gain of stability with increasing spatial scale). In addition, spatial correlation in temperature and vegetation structure synchronized bird population dynamics over space and thus decreased IAR slopes. By demonstrating the joint influence of functional traits and environmental factors on bird population stability across scales, our results highlight the need for dynamic conservation strategies tailored to particular types of species in an era of global environmental changes.

KEYWORDS

avian populations, environmental factors, invariability–area relationships, life history trait, migration

INTRODUCTION

Understanding the mechanisms underlying population stability is a key step in predicting species' responses to environmental change (Grman et al., 2010). Stability is a

multifaceted concept that can be measured in various ways, and a commonly used metric in ecological literature is invariability, defined as the ratio of mean to the standard deviation of some ecological property (e.g., population size or measurements of environmental covariates) over time (Donohue et al., 2016). In fluctuating environments, a higher invariability of population

Pubin Hong and Zhouyuan Li contributed equally.

dynamics signifies a more stable population with a lower risk of extinction (Schindler et al., 2010). While theoretical research has extensively documented how population invariability might be influenced by local and spatial factors, such as species interactions, dispersal, and environmental fluctuations, previous studies have mainly focused on two discrete spatial scales (local and regional) in fragmented and patchy landscapes (Abbott, 2011; Wang et al., 2015). To understand population stability across multiple scales, we need a more nuanced understanding of how population stability scales with the area, as well as the underlying drivers shaping these patterns in the context of habitat loss and climate change.

A novel approach to resolving these questions is offered by the invariability–area relationship (IAR), a concept explicitly proposed to characterize the spatial scaling of ecological stability (Wang et al., 2017). IAR describes how invariability changes as the study area increases, which is usually represented by a power law. On a log–log scale, the intercept of IAR reflects ecological stability at local scales (i.e., stability within one unit area), whereas the slope of IAR captures the increased rate of stability with the area (Figure 1). The approach of IAR offers a toolkit for understanding environmental impacts on population stability across scales, which has recently been adopted to explore the linkage between spatial scaling patterns of diversity and stability (Delsol et al., 2018; Zhang et al., 2018) and to address the scaling of other facets of stability, for example, resilience and resistance (Clark et al., 2021).

While ecological processes shaping local population invariability (i.e., IAR intercept) have been well documented (Isbell et al., 2015; Li et al., 2021), those driving the IAR slope are less understood. Theoretical models show that the IAR slope is intrinsically related to patterns of spatial synchrony between different populations across the landscape (Wang et al., 2017). Specifically, asynchronous population dynamics, characterized by a lower correlation between neighboring populations (hereafter low neighborhood synchrony) and/or a faster loss of synchrony with distance (hereafter high synchrony decay rate), can lead to a faster increase in stability with area, which is reflected by a larger IAR slope (Figure 1; Table 1). The reverse is also true. Therefore, resolving the processes underlying spatial synchrony patterns is the key to understanding the slope of IAR. Yet, it remains challenging to disentangle the underlying mechanisms of spatial population synchrony and stability in realistic systems, because they arise from a complex interplay of ecological processes operating at different scales (Delsol et al., 2018; Wang et al., 2017).

Both environmental and biotic factors have been documented to influence local population invariability

and spatial population synchrony, which translate into different patterns of IAR intercept and slope, respectively. Environmental factors generally fluctuate through time, and species populations seem likely to undergo larger fluctuations in more variable environments (Davis et al., 2002; Lande et al., 1999), implying a positive correlation between environmental invariability and the IAR intercept (Figure 1; Table 1). Moreover, different geographical locations often undergo correlated environmental fluctuations, particularly over short distances (Liebhold et al., 2004; Moran, 1953). Such correlated environmental conditions can synchronize population dynamics over space. For instance, Koenig and Liebhold (2016) found that an increase in spatial environmental correlation over recent decades caused increased spatial synchrony of over-wintering bird populations across North America. Moreover, the decreasing environmental correlation between sites separated by greater distances can cause a similar distance decay in spatial population synchrony (Hansen et al., 2020; Liebhold et al., 2004) (Figure 1; Table 1). Thus, we expect that neighborhood synchrony and synchrony decay rates of populations, respectively, should be positively related to those of environmental factors, which in turn affects the IAR slope (Figure 1; Table 1).

Biotic factors, particularly species functional traits, also regulate population dynamics over time and space (de Bello et al., 2021; Schnabel et al., 2021). Two categories of functional traits can be particularly relevant. The first category includes life history traits conceptualized as the “fast–slow” continuum (Cooke et al., 2019). Along this continuum, “fast” species are characterized by short lifespans, small body sizes, and high growth rates and fecundity, while “slow” species are characterized by long lifespans, large body sizes, and low growth rates and fecundity. In fluctuating environments, “fast” species can recover rapidly after disturbances and thus exhibit higher local population invariability (e.g., Li et al., 2021). In addition, theoretical and empirical studies have shown that “fast” species generally exhibit lower spatial synchrony between neighboring and more distant patches compared with “slow” species, because “fast” species dampen local population fluctuations before they propagate to other patches (Lande et al., 1999; Marquez et al., 2019; Paradis et al., 2000; Wang et al., 2015). Overall, we expect that scattered populations of “fast” species will be more locally stable (a higher IAR intercept) and exhibit a faster increase in stability with area (a higher IAR slope) due to lower neighborhood synchrony and higher synchrony decay rate (Figure 1; Table 1).

The second category of trait is related to species dispersal. Theoretical models predict that dispersal could increase spatial synchrony and local invariability of

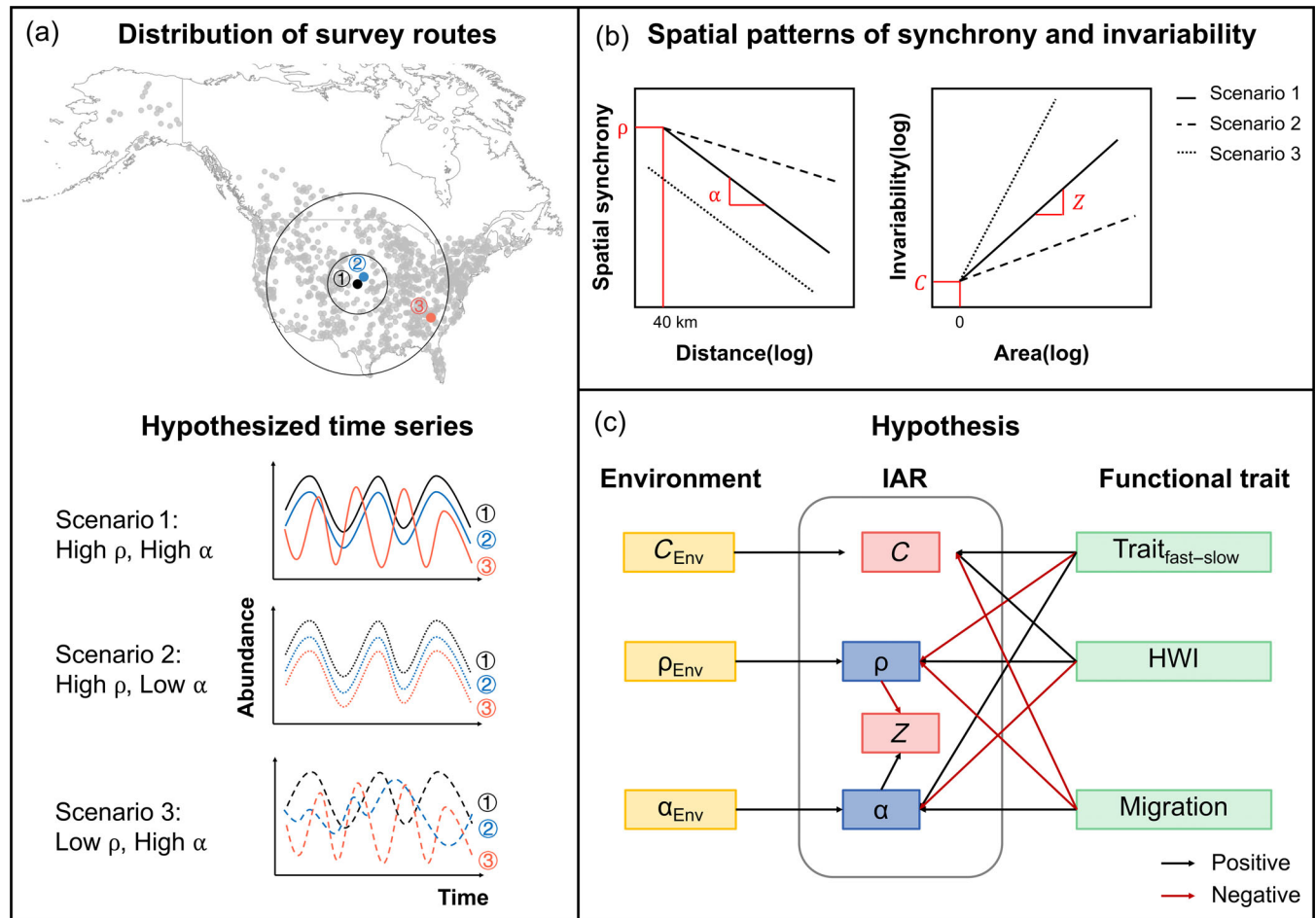


FIGURE 1 Conceptual diagrams illustrating the spatial patterns of population invariability and synchrony, as well as the hypothesized effects of biotic and environmental factors. The map of North America (a) shows the distribution of all 1035 bird survey routes (circles) included in this study. To construct the invariability–area relationship (IAR), we selected one route (e.g., Route 1) and then increase the sampling area to include next-nearest (e.g., Route 2) and more distant (e.g., Route 3) populations. Populations of a given species fluctuate over time at each locality, and these fluctuations are correlated among routes, with higher correlations (or synchrony) between neighboring routes (e.g., Routes 1 and 2) than between more distant routes (e.g., routes 1 and 3). In Scenario 1, synchrony is high between neighboring routes (large ρ) but decreases quickly as distance increases (large α). In Scenario 2, synchrony is high between neighboring routes (large ρ) and decreases slowly as distance increases (small α). In Scenario 3, synchrony is relatively low between neighboring routes (small ρ) and decreases quickly as distance increases (large α). (b) The relationships between spatial synchrony and distance and IAR under the above three scenarios. The synchrony–distance relationships are captured by two parameters, that is, synchrony between two routes with a distance of 40 km (i.e., ρ , neighborhood synchrony) and the decay rate of synchrony with distance (i.e., α , synchrony decay rate). IARs are also captured by two parameters, that is, the intercept (C) and slope (Z). Theoretically, Z decreases as ρ increases, and increases as α increases. (c) A hypothesized structural equation model showing the potential effects of functional traits and environmental factors on synchrony–distance relationships and IAR. Functional traits include Trait_{fast-slow} (i.e., the fast–slow life history trait spectrum), hand-wing index (HWI; a proxy for dispersal ability), and migration. Environmental factors include average summer temperature, precipitation, and leaf area index. C_{Env} , ρ_{Env} , and α_{Env} represents the IAR intercept, neighborhood synchrony, and synchrony decay rate for the respective environmental factor. See Table 1 for the rationale underlying each hypothesized effect.

populations (Abbott, 2011; Liebhold et al., 2004; Wang et al., 2015). In particular, dispersal is predicted to synchronize population dynamics between both neighboring and distant locations (Lande et al., 1999), in line with observational data from birds and fishes (Chevalier et al., 2014; Paradis et al., 1999), as well as microcosm experiments (Dey & Joshi, 2006). We therefore predict

that dispersal will increase the IAR intercept (i.e., local population invariability) but decrease the IAR slope (i.e., the increased rate of invariability with area) due to the increased neighboring synchrony and decreased synchrony decay rate driven by dispersal (Figure 1; Table 1).

Birds are sensitive to environmental change (Burger & Gochfeld, 2004). Recent studies have demonstrated that

TABLE 1 Hypotheses predicting the effects of functional traits and environmental factors on synchrony–distance and invariability–area relationships (IAR).

Pathway	Hypotheses and mechanisms
$\rho \rightarrow Z (-)$	More synchronous fluctuations of neighborhood populations provide weaker spatial insurance effects for stability at larger scales and thus slow down the increase of invariability with area (Wang et al., 2017).
$\alpha \rightarrow Z (+)$	A faster decay of population synchrony with distance indicates more asynchronous dynamics among scattered populations, which provides stronger spatial insurance effects and thereby accelerates the increase in invariability with area (Wang et al., 2017).
Trait _{fast-slow} → $\rho_{\text{Species}} (-)$	In fluctuating environments, “fast” species could dampen population fluctuations locally before they disperse to other patches, which thus have lower neighborhood synchrony and higher synchrony decay rate (Lande et al., 1999; Marquez et al., 2019; Paradis et al., 2000; Wang et al., 2015).
Trait _{fast-slow} → $\alpha_{\text{Species}} (+)$	
Trait _{fast-slow} → $C (+)$	“Fast” species have high reproductive output, recovering more rapidly after perturbations, with populations therefore more stable than “slow” species (Wang et al., 2015).
HWI → $\rho (+)$	Species with larger HWI tend to have higher dispersal capacity (Weeks et al., 2022), which can increase spatial synchrony between neighboring patches and over longer distances, that is, a slower decay of synchrony with distance (Chevalier et al., 2014; Lande et al., 1999; Paradis et al., 1999).
HWI → $\alpha (-)$	
HWI → $C (+)$	Species with larger HWI tend to have higher dispersal capacity, which can increase local population invariability due to spatial rescue effects (Abbott, 2011; Wang et al., 2015).
Migration → $\rho (-)$	Migratory species have lower neighborhood synchrony and higher synchrony decay rate because seasonal travel periodically reshuffles populations among locations across years (Finch et al., 2017), thus decreasing spatial synchrony between neighboring and distant locations.
Migration → $\alpha (+)$	
Migration → $C_{\text{IAR}} (-)$	Migratory species have lower local population invariability because long-distance migration exposes the population to unpredictable environmental conditions, increasing the stochasticity of population dynamics (Carey, 2009; Klaassen et al., 2014; Rushing et al., 2020).
$\rho_{\text{Env}} \rightarrow \rho (+)$	A higher spatial correlation in the environment should cause a higher spatial synchrony of populations, referred to as the Moran effect (Hansen et al., 2020; Liebhold et al., 2004).
$\alpha_{\text{Env}} \rightarrow \alpha (+)$	A faster decay of spatial correlation in the environment with distance should cause a faster decay of spatial population synchrony with distance (Koenig, 2002; Lande et al., 1999).
$C_{\text{Env}} \rightarrow C (+)$	A higher environmental fluctuation decreases the invariability of local population dynamics (Davis et al., 2002; Lande et al., 1999).

Note: Parameters α and ρ denote the slope (synchrony decay rate) and intercept (neighborhood synchrony) of synchrony–distance relationships, respectively. Parameters Z and C denote the slope and intercept of IAR, respectively. Parameters without subscript correspond to bird populations; those with subscript “Env” correspond to environmental factors. Trait_{fast-slow} represents the fast–slow life history trait spectrum; HWI is the hand-wing index, a morphological correlate of dispersal ability in birds; migration indicates migratory status. Each pathway corresponds to one arrow in the structural equation model in Figure 1c.

populations of North American bird species have been declining significantly in the face of numerous anthropogenic threats (Rosenberg et al., 2019) and displayed increased spatial synchrony due to an increasingly synchronized temperature (Koenig & Liebhold, 2016). Resolving the mechanisms of bird population stability from local to regional scales is key to predicting their responses to future environmental changes and informing conservation planning (Catano et al., 2020). For birds, an additional factor relevant to spatial population dynamics is their migratory behavior, a strategy for coping with seasonal variations in resources and climate (Dingle & Drake, 2007). The flip side of migration is that long-distance travel also exposes populations to greater environmental heterogeneity and numerous risks which may increase individual mortality,

introducing uncertainty into population dynamics (Carey, 2009; Klaassen et al., 2014; Rushing et al., 2020). Thus, we predict that migratory species have lower local population invariability (i.e., a lower IAR intercept) but a faster increase of stability with area (i.e., a higher IAR slope) due to lower spatial synchrony between neighboring and more distant locations because seasonal movements may periodically reshuffle populations among locations over time (Finch et al., 2017) (Figure 1; Table 1).

Here, we examine the patterns and determinants of bird population stability across North America using long-term continent-wide breeding survey data for 249 widespread species. We investigated how environmental factors and functional traits regulate the spatial scaling patterns of bird population stability, characterized by the

intercept and slope of IAR. Our hypotheses are summarized in Table 1 and illustrated in Figure 1. In revealing patterns and determinants of bird population stability over space and time, our results offer a roadmap for using IAR to predict and monitor how bird species with different traits respond to environmental change, with implications for the design of targeted species conservation strategies.

METHODS

Data sources

We obtained bird population time series data from the North American Breeding Bird Survey (BBS) (Pardieck et al., 2018). BBS contains annual surveys at over 4000 transects (or survey routes) in the USA and Canada, each of which have reported the abundance of all bird species observed during each breeding season (June–July) since 1966. The average lengths of the survey route is 39.4 km; each route includes 50 locations where observers recorded bird species and abundance within a 0.4-km radius. We excluded all routes with fewer than 15 years of continuous observations, resulting in a total of 1035 routes sampled from 1999 to 2013. To analyze the spatial scaling of stability, we focused on species encountered in ≥ 64 routes (i.e., 2^6 , which gives at least seven levels of area [$2^0, 2^1, \dots, 2^6$] for calculating IAR). In total, we obtained data from 249 species for subsequent analyses.

Using published datasets (Myhrvold et al., 2016; Wilman et al., 2016), we compiled information on four functional traits to capture the fast–slow continuum of avian life history: body mass (g), fecundity (i.e., the total annual number of eggs laid), duration of nesting time (i.e., combined length of incubation and fledging periods), and lifespan (years). In addition, we obtained the hand-wing index (HWI) and migratory status of all study species from Sheard (2020). We used HWI as a surrogate for species dispersal ability and natal dispersal distance (Weeks et al., 2022). Of the 249 species studied, 214 were migratory and 35 nonmigratory. One species (*Troglodytes pacificus*) lacked data on HWI and was, therefore, removed from HWI-related analyses. For six species missing lifespan information, we used the “imputePCA” function in the *missMDA* package (Josse & Husson, 2016) to estimate their position on the fast–slow spectrum (see below).

Three environmental variables (mean temperature, mean precipitation, and leaf area index during summer) were used to describe temporal and spatial environmental variability. We obtained monthly air temperature and precipitation data at a spatial resolution

of 0.5° from the National Oceanic and Atmospheric Administration–Climate Anomaly Monitoring System (Fan & van den Dool, 2008) and Global Precipitation Climatology Center (Schneider et al., 2018), respectively. To assess vegetation cover linked to food supply and habitat structure, we obtained a monthly leaf area index at a spatial resolution of 0.05° from the National Earth System Science Data Center of the National Science & Technology Infrastructure of China (Xiao et al., 2016). For each survey route, we extracted monthly environmental records from these data sources, and then took the mean (for temperature and leaf area index) or sum (for precipitation) of the monthly records from June to August to estimate relevant environmental conditions throughout the bird survey. Data sources are provided in Appendix S1: Table S1.

Defining the fast–slow continuum of life history

We derived a fast–slow continuum by conducting a principal components analysis (PCA) on four functional traits: body mass, nesting duration, lifespan, and fecundity. The first axis of PCA explained 62.8% of total variation and can be interpreted as the fast–slow continuum (denoted as $\text{Trait}_{\text{fast–slow}}$; Appendix S1: Figure S1). That is, species with larger values of $\text{Trait}_{\text{fast–slow}}$ (i.e., fast species) were characterized by smaller body mass, shorter nesting duration and lifespan, and higher fecundity, and species with smaller values of $\text{Trait}_{\text{fast–slow}}$ (i.e., slow species) were characterized by larger body mass, longer nesting period and lifespan, and lower fecundity. PCA was implemented in the *FactoMineR* R package (Lê et al., 2008).

Calculation of IAR and synchrony–distance relationships

We constructed the IAR by calculating population invariability with accumulating numbers of survey routes. For each species, we first extracted all routes where the focal species were encountered (ranging from 74 to 964 for different species); subsequently, we randomly selected one route as the starting point and then increased the number of routes by including the next-nearest route(s) to 2, 4, 8, 16, ..., to the total number of routes occupied by the focal species. For each given area or number of routes (A), we defined population invariability ($\text{Inv}(A)$) as the inverse of the coefficient of variation of population size (Wang et al., 2017): $\text{Inv}(A) = \frac{\mu}{\sigma}$, where μ and σ are the temporal mean and standard deviation, respectively, of

the total population size of the focal species within study area A over the period 1999–2013. To avoid biases arising from the uneven distribution of routes, we repeated this procedure 100 times for each species using different routes as the starting point, thus obtaining 100 values of population invariability at each level of area. For each level of area, we derived the average invariability using the harmonic mean of invariability across 100 replicates weighted by the corresponding total population size (Wang et al., 2019). To derive the slope and intercept of IAR for each species, we fitted a linear model of IAR on a log–log scale:

$$\log_{10}(\overline{Inv(A)}) \sim Z \cdot \log_{10}(A) + C \quad (1)$$

where $\overline{Inv(A)}$ represents the average invariability for a study area A , and Z and C represent the slope and intercept of IAR, respectively.

For each species, we calculated the spatial synchrony of bird population size between all pairs of routes. Spatial synchrony (ρ) was defined as the temporal correlation coefficient in population sizes between a pair of routes. We first classified all pairs of routes into different categories according to their distances ($D < 10$ km, 10–100 km, 100–1000 km, > 1000 km). Then we divided each distance category (except for $D < 10$ km) equally into five subcategories and calculated the average synchrony ($\overline{\rho(D)}$) for each distance subcategory. We fitted a linear model between average synchrony and distance on the log–log scale:

$$\log_{10}(\overline{\rho(D)}) \sim -\alpha \cdot \log_{10}\left(\frac{D}{D_0}\right) + \rho \quad (2)$$

where the slope α captures the decay rate of spatial synchrony with distance (i.e., synchrony decay rate), and ρ represents the spatial synchrony between two neighboring routes (i.e., neighborhood synchrony). Because the median distance between the nearest routes is 40.45 km, we used $D_0 = 40$ km to calculate neighborhood synchrony.

Similarly, for each species, we calculated the IAR and synchrony–distance relationship for each environmental variable (temperature, precipitation, and leaf area index) within the set of routes in which the focal species was encountered. We then extracted the fitted parameters of Z , C , α and ρ for each environmental variable with respect to each species for subsequent analyses. We added subscripts “temp,” “prep,” and “LAI” (leaf area index), respectively, to these parameters when referring to the corresponding environmental factor to distinguish them from each other and from species parameters.

Statistical analyses

We used linear regression models to fit IAR (Equation 1) and synchrony–distance relationships (Equation 2), and to obtain the intercept and slope of IARs and the neighborhood synchrony and synchrony decay rate for each species and each environmental variable. We then used linear mixed-effects models (Pinheiro et al., 2022) to obtain the overall trends of IAR and synchrony–distance relationships, with species as the random effect. With all relevant parameters fitted, we examined how neighborhood synchrony and synchrony decay rate were related to the slope of IAR across species. We then used linear regression models to test the effects of functional traits and environmental variables on the intercept and slope of IAR of bird species and their neighborhood synchrony and synchrony decay rates. We also fitted quadratic regression models to test possible nonlinearity (i.e., whether the quadratic term is significant). For the binary migration variable (migratory versus nonmigratory), we assessed its effect using a t -test. Finally, we constructed a structural equation model (SEM) to examine whether functional traits and environmental variables affected IAR directly or indirectly via influencing the synchrony–distance relationship. Our initial SEM (Figure 1c) was constructed according to the hypotheses summarized in Table 1. After fitting the SEM using the R package *piecewiseSEM* (Lefcheck, 2016), we removed non-significant paths and variables and obtained a final SEM. We calculated the net effects on the IAR intercept and slope of each functional trait or environmental variable. All statistics were conducted in R version 4.0.3 (R Core Team, 2020).

RESULTS

All bird species showed positive IAR, with IAR slopes varying from 0.072 to 0.456 across species (mean = 0.293; Figure 2). The IAR slope was negatively correlated with the IAR intercept ($r = -0.23$, $N = 249$, $p < 0.001$; Figure 2b). Most species exhibited negative spatial synchrony–distance relationships (Appendix S1: Figure S2). As expected, the IAR slope was positively related to the synchrony decay rate ($r = 0.56$, $N = 249$, $p = 0.002$), and negatively related to neighborhood synchrony ($r = -0.20$, $N = 249$, $p < 0.001$) (Appendix S1: Figure S2). While different species varied markedly in the number of routes where they were encountered (from 74 to 964 routes), this variable had no effect on the intercept or slope of IAR, neighborhood synchrony or synchrony decay rate ($p > 0.1$ for all; Appendix S1: Figure S3).

Functional traits related to fast–slow life history (hereafter, fast–slow traits) were positively associated with the

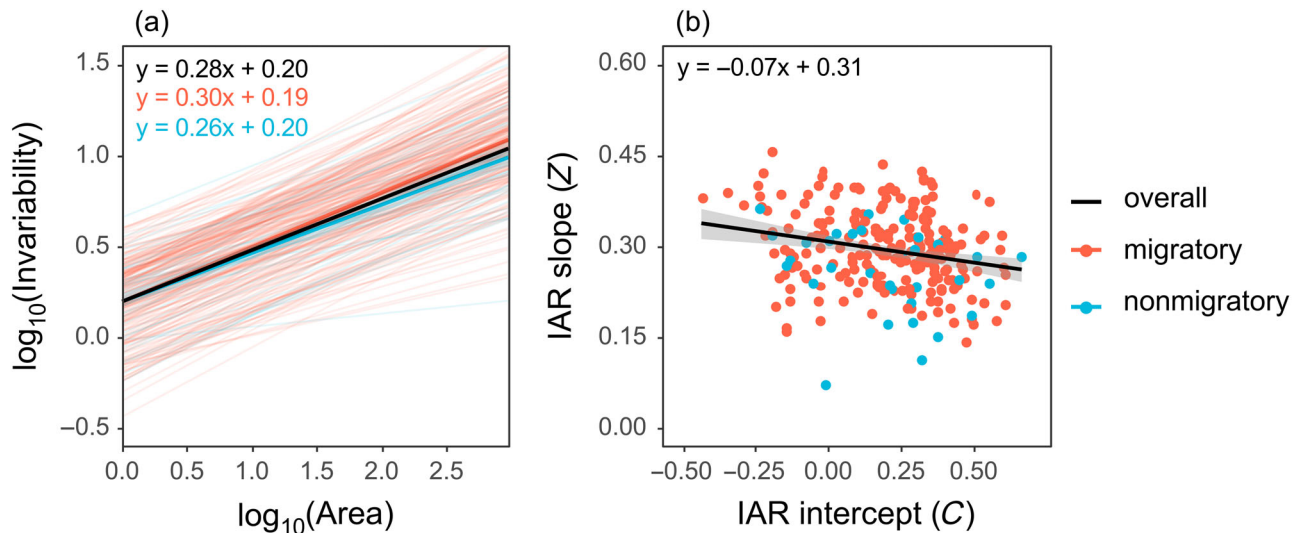


FIGURE 2 Invariability–area relationships (IAR) of bird populations across North America. Results shown are (a) IAR models fitted for each species and (b) the relationships between slope (Z) and intercept of IAR (C) across species. Red and blue colors show migratory and nonmigratory species, respectively. In (a), each light-colored line describes the IAR for one species. The black line represents the overall IAR across all species fitted by a linear mixed-effects model, and red and blue lines represent overall IARs for migratory and nonmigratory species, respectively. In (b), each point shows the intercept and slope of IAR for one species. The black line is fitted by simple regression. For all regressions, $N = 249$ and $p < 0.001$ for the slope.

IAR intercept ($r = 0.55$, $N = 249$, $p < 0.001$), but they were not related to the IAR slope ($r = 0.02$, $N = 249$, $p = 0.802$) due to their positive associations with both synchrony decay rate ($r = 0.12$, $N = 249$, $p = 0.064$) and neighborhood synchrony ($r = 0.13$, $N = 249$, $p = 0.041$) (Figure 3; Appendix S1: Figure S4). Similar relationships were found using the four individual traits related to life history (Appendix S1: Figure S5). HWI was negatively correlated with IAR intercept ($r = -0.48$, $N = 248$, $p < 0.001$), but not related to IAR slope and patterns of spatial synchrony ($N = 248$, $p > 0.1$ for all) (Figure 3; Appendix S1: Figure S4). Migratory species tended to have larger IAR slopes than nonmigratory species ($t = 2.837$, $df = 44.4$, $p = 0.007$; Figure 3f). In alignment with this result, we also found that migratory species had lower neighborhood synchrony than nonmigratory ones ($t = -2.603$, $df = 36.4$, $p = 0.013$; Appendix S1: Figure S4), but similar synchrony decay rates ($t = 0.213$, $df = 49.7$, $p = 0.832$; Appendix S1: Figure S4). Migratory and nonmigratory species did not differ in their IAR intercept ($t = -0.116$, $df = 45.1$, $p = 0.908$; Figure 3c).

Environmental factors were also correlated with spatial synchrony patterns and IAR of bird populations (Figure 4). Spatial synchrony of mean temperature, mean precipitation, and leaf area index during summer all decreased with distance (Appendix S1: Figure S6). The neighborhood synchrony of bird populations was positively correlated with those of summer temperature, precipitation, and leaf area index ($p < 0.05$ for all; Figure 4c). However, we found no relationship between the

synchrony decay rate of bird populations and those of environmental variables ($p > 0.1$ for all; Figure 4d). The IAR intercept of bird populations was positively related to those of summer temperature and leaf area index ($p < 0.05$ for both; Figure 4a), but no relationship was found for the IAR slope ($p > 0.05$ for all three environmental variables; Figure 4b).

Our final SEM illustrated multiple pathways along which species traits and environmental variables jointly regulated the IAR of avian populations (Figure 5). Fast–slow traits were positively associated with the IAR intercept, and influenced the slope of IAR through two pathways: (i) by increasing the synchrony decay rate that was positively related to IAR slope; and (ii) by increasing neighborhood synchrony that was negatively related to IAR slope. These two pathways offset each other, resulting in a net weak, negative effect of fast–slow traits on the IAR slope (Figure 5). HWI was negatively associated with the IAR intercept, but not related to spatial synchrony patterns and IAR slope. Migratory species tended to have lower neighborhood synchrony and thus higher IAR slopes. Higher neighborhood synchrony of both temperature and leaf area index was associated with increased neighborhood synchrony for bird populations, and thus decreased IAR slope.

DISCUSSION

By revealing the IAR of breeding bird populations in North America, we have shown that a combination of

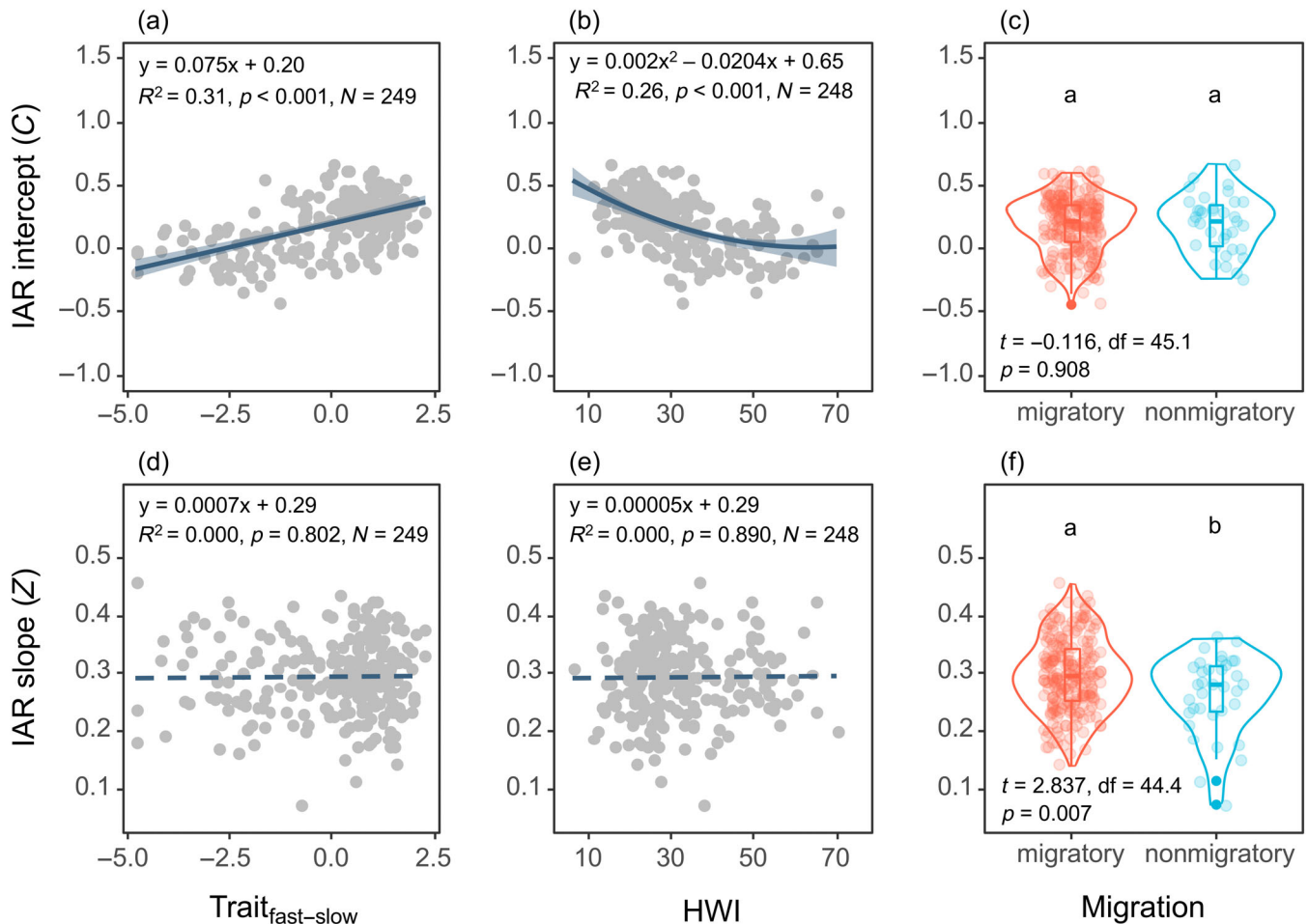


FIGURE 3 Effects of functional traits on invariability–area relationships (IAR). Panels show the intercepts (a–c) and slopes (d–f) of IAR for bird populations across North America. (a, d) Trait_{fast-slow} represents the fast–slow life history trait spectrum. (b, e) HWI represents the hand-wing index, which provides an index of dispersal ability. (c, f) Migration indicates whether a species is migratory or nonmigratory. In (a, b, d, e), a regression line is shown (solid line, $p < 0.05$; dashed line, $p > 0.05$) if the quadratic term is nonsignificant, otherwise a parabola curve is shown. In (c, f), different letters indicate significant differences between migratory and nonmigratory species ($p < 0.05$).

species functional traits and environmental factors jointly determine population stability at local scales (i.e., IAR intercept) and its scaling patterns over space (i.e., IAR slope). We found that local population stability is higher for bird species with “fast” life history strategies and lower flight efficiency, whereas the slope along which population stability increases with area is higher for “slow” species or migratory species, and when spatial correlation in temperature and leaf area index is low. Our results have useful implications for understanding the scaling properties of bird populations and predicting their responses to environmental changes.

Role of functional traits in regulating IAR of bird populations

Consistent with our hypotheses (Table 1), we found that “fast” species had higher local population invariability and

higher synchrony decay rate than “slow” species (Figure 3; Appendix S1: Figure S4). However, contrary to our expectation, “fast” species also exhibited higher neighborhood synchrony. This might be explained by the high sensitivity (or lower resistance) to environmental variations of “fast” species compared with “slow” ones (Li et al., 2021). In a spatially correlated environment, local populations of “fast” species track environmental fluctuations more closely and thereby exhibit higher spatial synchrony (Trzcinski et al., 2008). Alternatively, the trend in neighborhood synchrony along the fast–slow spectrum may be complicated by time series length in empirical data. Metapopulation theory predicts that “fast” species could exhibit higher spatial synchrony if time series are short, although the opposite pattern was expected over long periods (Luo et al., 2021). Because the neighborhood synchrony and synchrony decay rate had opposite relationships with the slope of IAR, “fast” species had similar, albeit slightly lower, IAR slopes as “slow” species in our analyses.

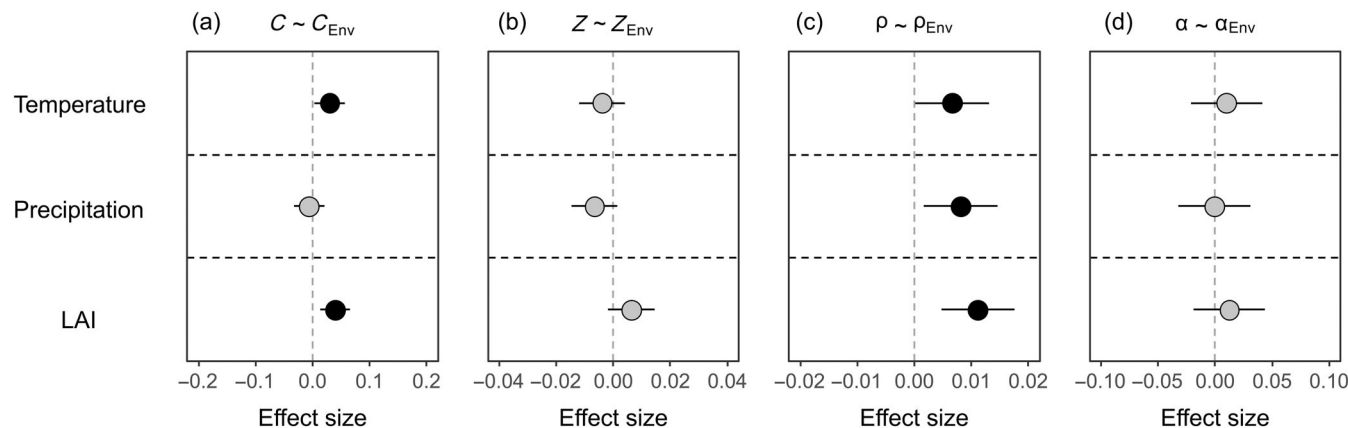


FIGURE 4 Effects of environmental factors on invariability–area relationships (IAR). Panels show effect sizes (mean ± 95% CI) of environmental factors on the intercepts (a) and slopes (b) for IAR of avian populations across North America, as well as on their neighborhood synchrony (c) and synchrony decay rates (d). For each parameter of IAR and synchrony–distance relationships, the explanatory variables are the respective parameters of the three environmental variables; for example, in (a), the response variable is the IAR intercept of bird populations, and the explanatory variables are the IAR intercepts of temperature, precipitation, and leaf area index. Effect sizes are standardized coefficients from simple regressions. Confidence intervals not overlapping zero indicate significant effects ($p < 0.05$; highlighted in black).

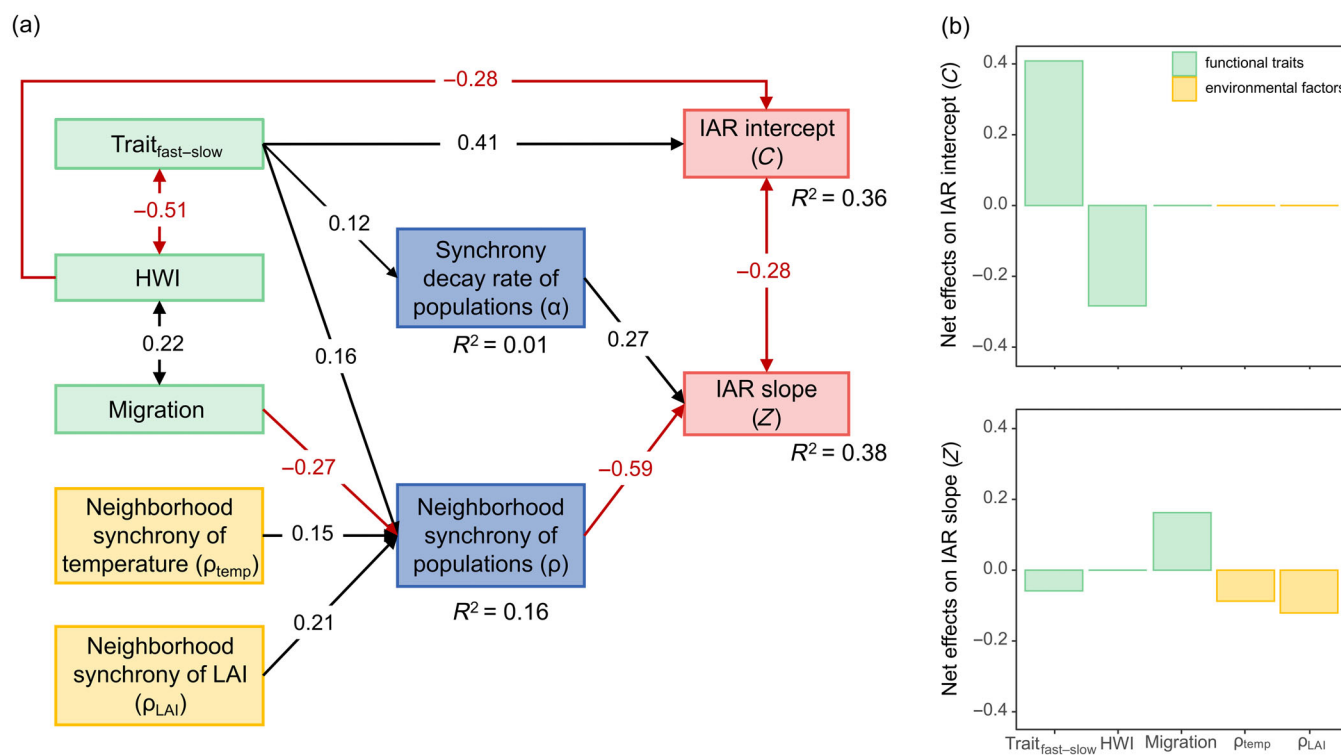


FIGURE 5 Structural equation model depicting the direct and indirect effects of functional traits and environmental factors on invariability–area relationships (IAR) (a) and their net effects (b). Trait_{fast–slow} represents the fast–slow life history trait spectrum; HWI represents the hand-wing index; and migration denotes migratory status. ρ_{temp} and ρ_{LAI} represented neighborhood synchrony of summer temperature (temp) and leaf area index (LAI), respectively. Model fit was good (Fisher’s $C = 28.76$; $df = 32$; $p = 0.58$).

We found that populations of bird species with higher HWI were less stable at the local scale (i.e., low IAR intercept), and HWI did not affect the spatial synchrony of populations and the IAR slope (Figures 3 and 5).

These results contradict our expectations and challenge the theoretical prediction that dispersal has both local stabilizing and spatial synchronizing effects. One explanation may be that HWI provides only a crude metric of

dispersal. While recent studies have demonstrated a significant relationship between HWI and avian dispersal potential, including natal dispersal distance (Claramunt, 2021; Weeks et al., 2022), HWI is partly related to foraging behaviors disconnected from dispersal. Even if HWI does estimate variation in dispersal capacity, the realized dispersal rate can be modulated by biotic and abiotic environments, making it less predictable from morphological indices. In addition, our results may reflect a relatively weak connection between dispersal and population parameters. Although the concept that dispersal can decrease local population variability and increase spatial synchrony makes intuitive sense and is generally predicted by simple metapopulation models (e.g., Abbott, 2011; Wang et al., 2015), the effects of dispersal may be subtle and dependent on modes of dispersal (e.g., symmetric/asymmetric, costly/cheap), as well as on species interactions, spatial and temporal environmental heterogeneity, and timescale (Bowler & Benton, 2011; Luo et al., 2021; Wang et al., 2015). Indeed, a recent meta-analysis revealed weak support for the local stabilizing and spatially synchronizing effects of dispersal (Yang et al., 2022).

The finding that migratory species exhibited a higher IAR slope and lower neighborhood synchrony than nonmigratory species is consistent with our predictions and also aligns with a recent study showing that individuals from long-distance migratory bird populations tended to spread out and mix with individuals from different populations from year to year (Finch et al., 2017). However, contrary to our hypothesis that migratory species are locally less stable than nonmigratory species, they showed no difference in local population invariability. This is possibly explained by the fact that migratory species escape from locally harsh environments and avoid the influences of local environmental fluctuations (Winger et al., 2019), although they experience high mortality during migration travels (Klaassen et al., 2014).

Environmental controls on IAR

Environmental factors have long been documented to regulate population dynamics at local scales and generate spatial population synchrony at larger scales (Hansen et al., 2020; Koenig, 2002; Moran, 1953). Partially confirming this proposition, we found that the neighborhood synchrony of bird populations was positively related to those of summer temperature and leaf area index (but not precipitation), whereas neither synchrony decay rates nor local invariability of bird populations was related to that of any environmental factor. For birds, temperature is an important abiotic environmental factor influencing their growth, reproduction, migration, and annual cycle, particularly at higher latitudes

(Carey, 2009). Leaf area index characterizes the state and density of vegetation, which serves as the primary source of energy at the base of multitrophic food webs in which all bird species are embedded (Li et al., 2021; White et al., 2011). In comparison, precipitation had a weak effect on bird populations, consistent with a previous analysis showing a weaker synchronizing effect of precipitation on bird population dynamics than that of temperature (Koenig & Liebhold, 2016). This finding is also in line with previous studies showing that bird species vary in their responses to precipitation changes depending on local context (Brawn et al., 2017; Mares et al., 2017), with the strongest responses typically detected in “climate-sensitive” conditions (e.g., high altitude, high latitude or high aridity) (Ancill et al., 2014; Ewing et al., 2020; Mares et al., 2017). Our results suggest that an increasing spatial synchrony in temperature and/or leaf area index leads to increased spatial population synchrony and thus lower IAR slopes in birds, a factor associated with reduced population persistence (i.e., through extinction events arising from simultaneous population declines).

We found relatively weak effects of local environmental invariability (i.e., the ratio of mean to standard deviation of an environmental factor, in this case summer temperature and leaf area index) on the local stability of bird populations. It is possible that population stability at the transect scale is influenced by other factors not considered in our analyses, for example, fluctuations in resource availability and shifts in habitat structure associated with urbanization or other forms of land-use change (Koenig et al., 2009; Olivier et al., 2020). A reduced impact of environmental factors may also reflect our choice of study system. Most of our study species are widespread in North America, where they experience a large gradient of environmental conditions, making them better adapted to extreme environments (Cohen et al., 2020). In other words, our analyses focus on a subset of bird species relatively less sensitive to environmental variations than, for example, tropical birds (Ghalambor et al., 2006).

Caveats

Whereas long-term data from the North American BBS provide an excellent opportunity to uncover the spatial scaling patterns of natural population stability, there are limitations in data quality or coverage that may affect our results. For example, the dataset includes observational errors in population records (Farmer et al., 2014), particularly for large-bodied species with relatively small population sizes (“slow” species in our analysis) and more mobile species (species with larger HWI). Such biases can cause an underestimation of local population stability

and spatial synchrony. In addition, the exclusion of rarer species and the relatively narrow geographical focus of our sampling means that many study species overlap substantially in their distributional ranges, reducing variation in environmental conditions and climatic invariability across species. Further studies are needed to examine patterns of IAR based on higher resolution data across a wider spectrum of environmental conditions, ideally including the tropics when comparable surveys exist.

CONCLUSIONS

The invariability–area relationship was proposed as an intuitive tool to characterize the spatial scaling of population stability and further inform management and conservation planning. The analyses presented here pave the way toward these applications by exploring the patterns and determinants of IAR across North American bird populations. Our findings demonstrate that functional traits and environmental factors jointly predict patterns of population stability across spatial scales, thereby establishing a framework for understanding the response of biodiversity to environmental change and designing species-specific conservation strategies. For example, patterns of IAR suggest that direct conservation action focused on maintaining local population sizes is more appropriate for species with slow life history dynamics and larger HWI as these have lower local population stability. Conversely, management interventions focused on preserving habitat at the wider landscape scale are more appropriate for species with larger IAR slope, such as migratory birds. Patterns of IAR in North American birds also support the view that the goal of species conservation can best be achieved through the preservation of spatial heterogeneity in vegetation type, which appears to stabilize population dynamics and reduce the risk of population collapse at large scales.

AUTHOR CONTRIBUTIONS

Shaopeng Wang conceived the idea; Pubin Hong and Zhouyuan Li performed the study; Pubin Hong, Zhouyuan Li, and Qi Yang assembled and analyzed the data, with help from Wanlu Deng, Yanjie Xu, Joseph A. Tobias, and Shaopeng Wang; Pubin Hong, Zhouyuan Li, and Shaopeng Wang wrote the first draft of the manuscript; Joseph A. Tobias contributed substantially to the revision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Hong, 2022) are available in Figshare at <https://doi.org/10.6084/m9.figshare.21541560.v2>. This manuscript uses previously published data as summarized in Appendix S1: Table S1. The query details for air temperature and leaf area index data sets used for this research are summarized in Appendix S1: Table S1.

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SUPPORTING INFORMATION

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