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# Functional Ecology

Title:

## Composition of 'fast-slow' traits drives avian community stability over North America

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### AUTHORS' CONTRIBUTIONS

Shaopeng Wang and Zhouyuan Li conceived the idea and designed methodology; Zhouyuan Li and Heng Zhang collected the data; Zhouyuan Li, Heng Zhang, Shaopeng Wang, and Yanjie Xu analysed the data; Zhouyuan Li and Shaopeng Wang led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### DATA ACCESSIBILITY

Data can be accessed through the North American Breeding Bird Survey

(<https://www.pwrc.usgs.gov/BBS/RawData/>), traits (<https://dx.doi.org/10.6084/m9.figshare.c.3306933>), and

environment (<http://iridl.ldeo.columbia.edu/>; <http://mpimet.mpg.de/cdi>;

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<http://www.geodata.cn/thematicView/GLASS.html>)

#### **CONFLICT OF INTEREST STATEMENT**

All authors declare that there is no conflict of interest.

#### **Biosketch**

The Theoretical Ecology Lab, led by Dr. Shaopeng Wang, at the Institute of Ecology at Peking University combines theory and data analysis to understand biodiversity and ecosystem functioning and stability across scales and trophic levels. Dr. Zhouyuan Li focused on biodiversity-stability relationships in the context of global change.

Links to authors' web pages:

<http://scholar.pku.edu.cn/spwang>;

[https://www.researchgate.net/profile/Zhouyuan\\_Li2](https://www.researchgate.net/profile/Zhouyuan_Li2).

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## **Composition of ‘fast-slow’ traits drives avian community stability over North America**

**Running title: ‘Fast-slow’ traits drive avian community stability**

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## ABSTRACT

1. Rapid biodiversity loss has triggered decades of research on the relationships between biodiversity and community stability. Recent studies highlighted the importance of species traits for understanding biodiversity-stability relationships. The species with high growth rates ('fast' species) are expected to be less resistant to environmental stress but recover faster if disturbed; in contrast, the species with slow growth rates ('slow' species) can be more resistant but recover more slowly if disturbed. Such a 'fast-slow' trait continuum provides a new perspective for understanding community stability, but its validity has mainly been examined in plant communities. Here, we investigate how 'fast-slow' trait composition, together with species richness and environmental factors, regulate avian community stability at a continental scale.
2. We used bird population records from the North American Breeding Bird Survey during 1988-2017 and defined avian community stability as the temporal invariability of total community biomass. We calculated species richness and the community weighted mean (CWM) and functional diversity (FD) of four key life-history traits, including body size, nestling period (i.e. period of egg incubation and young bird fledging), life span, and clutch size (i.e. annual total number of eggs). Environmental factors included temperature, precipitation and leaf area index (LAI).
3. Our analyses showed that avian community stability was mainly driven by the CWM of the 'fast-slow' trait. Communities dominated by 'fast' species (i.e. species with small body size, short nestling period and life span, and large clutch size) were more stable than those dominated by 'slow' species (i.e. species with large body size, long nestling period and life span, and small clutch size). Species richness and the FD of the 'fast-slow' trait explained much smaller proportions of variation in avian community stability. Temperature had direct positive effects on avian community stability, while precipitation and leaf area index affected community stability indirectly by influencing species richness and trait composition.
4. Our study demonstrates that composition of 'fast-slow' traits is the major biotic driver of avian community stability over North America. Temperature is the most important abiotic factor, but its effect is weaker than that of the 'fast-slow' trait. An integrated framework combining 'fast-slow' trait composition and temperature is needed to understand the response of avian communities in a changing environment.

## KEYWORDS

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biodiversity, avian, North America, species stability, community stability, species asynchrony, community weighted mean, functional diversity, 'fast-slow' trait

Accepted Article

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## 1 | INTRODUCTION

Rapid biodiversity loss has stimulated decades of research to understand the relationship between biodiversity and community stability (Donohue et al., 2016; Ives & Carpenter, 2007; McCann, 2000). A great number of experiments have showed that species diversity can increase community stability over time, where stability was commonly defined as the ratio of the temporal mean to the standard deviation (i.e. inverse of the coefficient of variation) of some community property, e.g. biomass production (Hector et al., 2010; Isbell et al., 2015; Tilman, Reich, & Knops, 2006). One key mechanism underlying the stabilizing effect of biodiversity is that species exhibit asynchronous responses to environmental fluctuations, which compensate for each other and thus increase the stability of the total community (Thibaut & Connolly, 2013; Yachi & Loreau, 1999). While these studies offer useful insights for predicting the potential consequences of biodiversity loss, transferring results from biodiversity experiments into real-world ecosystems can be challenging because most previous studies encompassed small spatial scales, used limited taxonomic groups, and did not account for environmental gradients (De Laender et al., 2016; Gonzalez et al., 2020; Manning et al., 2019; van der Plas, 2019).

Existing biodiversity experiments have mostly been conducted at small spatial scales, in terms of both spatial extent and grain size. Grassland biodiversity experiments typically covered less than 10 ha, with plot size less than 400 m<sup>2</sup> (Craven et al., 2018; Isbell et al., 2015). Such small spatial scales may hardly match the scale at which biodiversity loss is happening and ecosystem management is concerned (Gonzalez et al., 2020). Biodiversity and stability, as well as their underlying mechanisms, are all scale dependent (Hubbell, 2001; Wang et al., 2017), making it unclear whether the diversity-stability relationship observed at small scales may extend to large ones (but see Wang et al. 2019). Several recent studies tested diversity-stability relationships at the landscape scale and found that biodiversity could stabilize ecosystem functions at larger scales, just as it did in local-scale experiments (McGranahan et al., 2016; Oehri, et al., 2020; Wang, et al., 2019; Wang et al., 2021; Wilcox et al., 2017). However, these studies focused mostly on plant communities. To test the generality of diversity-stability relationships at large scales, more studies are required to explore different taxa, particularly multitrophic communities because species at higher trophic levels are more susceptible to extinction (Binzer et al., 2011; Brose et al., 2017).

Avian species are global change indicator species due to their sensitivity to environmental changes (Burger & Gochfeld, 2004; Xu et al., 2019). A recent study showed that the populations of North American over-wintering birds underwent a significant

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increase in spatial synchrony during the past half century, possibly caused by an increased spatial synchrony of mean maximum temperature (Koenig & Liebhold, 2016). This increased spatial synchrony implies greater extinction risk and low regional-scale population stability (Earn, Levin, & Rohani, 2000; Wang & Loreau, 2016). More recently, a continental-scale evaluation concluded that North American bird populations had declined by 29% during the past half century (Rosenberg et al., 2019). Such a dramatic decrease in bird populations calls for an urgent need to better understand what drives avian species and community stability.

Based on long-term records of bird populations across North America, two recent studies showed that avian species diversity may contribute to avian community stability at different scales (Catano, Fristoe, LaManna, & Myers, 2020; Mikkelsen, McGill, Beaulieu, & Beukema, 2011). At the local scale (e.g. a sampling route with a length of 24.5km), species richness was positively related to the temporal stability of total bird numbers (Mikkelsen et al., 2011). At the regional scale (e.g. a state of the United States), Catano et al. (2020) showed that spatial community dissimilarity (i.e. species turnover across space) was positively related to spatial asynchrony and stability of community biomass at larger scales. These studies added new evidence for a positive diversity-stability relationship at larger spatial scales.

To reveal the biological mechanisms underlying diversity-stability relationships, a functional perspective has increasingly been adopted in recent studies of ecological stability (Craven et al., 2018; Lepš, et al., 2018; Májerková, et al., 2014). In particular, recent studies highlighted the value of the ‘fast-slow’ trait continuum for understanding species and community stability (Craven et al., 2018). Specifically, the ‘slow’ species, characterized by slower rates of resource uptake and growth, are more resistant to disturbance (Reich 2014), whereas the ‘fast’ species, characterized by rapid resource uptake and growth, are more resilient and recover faster from disturbances (Loreau & de Mazancourt 2013). The functional trait composition can be characterized using either the mean (e.g. community-weighted mean value, CWM) or variation (e.g. functional diversity, FD) of traits among species. Communities with a higher CWM of ‘fast-slow’ traits may exhibit higher, or lower, stability, depending on how species-level resistance and resilience balance. Moreover, communities with a higher functional diversity of ‘fast-slow’ traits benefit from the variety of traits and have higher stability (Craven et al. 2018).

Such a ‘fast-slow’ perspective bridges individual-level physiological and life-history processes such as metabolism, predation, and reproduction to community-level dynamics, which has broad implications for understanding diversity-stability relationships across different groups of organisms. For birds in our study, ‘fast’ species tend to have smaller body

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size, shorter life span and nestling period (i.e. period of egg incubation and young bird fledging), and larger clutch size (i.e. the annual total number of eggs). These characteristics of the ‘fast’ species result in lower resistance to environmental stress but a concomitant higher recovery rate if disturbed (Bird et al., 2020; Brose, Williams, & Martinez, 2006). In contrast, ‘slow’ species tend to have larger body size, longer life span and nestling period, and lower clutch size, which makes them less prone to be disturbed but recover more slowly (Hua, Fletcher Jr., Sieving, & Dorazio, 2013). The ‘fast-slow’ trait continuum thus provides a potentially useful tool to understand the stability of avian species and communities, but its validity has not been tested.

In this study, we used data from a long-term, continental-scale bird population survey (i.e. the North American Breeding Bird Survey) to examine the relative importance of species richness and functional trait composition on the stability of avian communities over North America. We characterized the community trait composition by both CWM and functional diversity of four bird traits that capture the ‘fast-slow’ continuum, namely body size, nestling period, life span, and clutch size. The temporal stability of biomass at both species and community levels were calculated. Our analysis covers a large spatial scale, in terms of both spatial extent (i.e. the continent of North America) and grain size (i.e., survey routes of 24.5 miles long, or 39.4 km long). As our data spans a large environmental gradient, we considered environmental variables as important covariates which could affect biodiversity and community stability (Figure 1) (Blüthgen et al., 2016; De Laender et al., 2016; Gilbert et al., 2020; van der Plas, 2019). We asked the following questions: (1) how are species richness and ‘fast-slow’ trait composition (i.e. CWM and functional diversity) related to avian community stability? (2) how environmental factors affect avian community stability directly and indirectly, through regulating species richness and ‘fast-slow’ trait composition?

## **2 | METHODS**

### **2.1 | Data sources**

The North American Bird Breeding Survey (BBS) has collected avian population data over the US and Canada ([www.pwrc.usgs.gov/bbs](http://www.pwrc.usgs.gov/bbs)) since 1966, in order to characterize the temporal dynamics of bird populations. Surveys were deployed annually at the peak of the breeding season (mostly in June) along more than 4000 sampling routes in the US and Canada. Survey routes parallel roads and are approximately 24.5 miles long, each consisting of 50 stops at a 0.5-mile interval. At each stop, a 3-minute counting was performed, during which all birds seen or heard within a 0.25 miles radius were recorded. For our analyses, we

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selected routes that were fully recorded during a 30-year period, i.e. 1988-2017. In total, 318 routes were selected along which 482 bird species were encountered (Figure S1).

To examine the effect of functional traits on bird community stability, we used four key life-history traits, including body size (i.e. the species-averaged individual mass), nestling period (i.e. the whole period of egg incubation and young bird fledging), life span, and clutch size (i.e. the annual total number of eggs in the nest). We retrieved these four traits for the 482 species mainly from two publicly accessible databases, i.e. EltonTraits 1.0 database (Wilman et al., 2014) and the amniote life-history database (Myhrvold et al., 2015), and supplemented information for any missing species from scientific publications and records (Table S1).

We collected monthly temperature data from the National Oceanic and Atmospheric Administration - Climate Anomaly Monitoring System (<http://iridl.ldeo.columbia.edu/sources/>), and monthly precipitation data from the Global Precipitation Climatology Centre (<http://mpimet.mpg.de/cdi>). Leaf area index (LAI) was extracted from the Advanced Very High Resolution Radiometer satellite imagery generated dataset of Global Land Surface Satellite (Xiao et al., 2013, 2016) from the platform of National Earth System Science Data Center, National Science & Technology Infrastructure of China (<http://www.geodata.cn>), as an indicator for local ecosystem productivity. Original temperature and precipitation data came in a NetCDF format for storing multi-dimensional digital matrices, which has a 30-day time resolution and a spatial resolution of  $0.5^\circ$  and  $0.25^\circ$ , respectively. LAI data was in an HDF format for storing raster image information, with an eight-day time resolution and a spatial resolution of  $0.05^\circ$ . Raster layers with a resolution of  $0.5^\circ$  were assembled and uniformly resampled using ArcGIS 10.0. These layers were overlaid with the shape file that contained longitude and latitude coordinates of the 318 survey routes. These point format layers contained temperature, precipitation, and LAI values for the 318 routes for the years 1988-2017. The 30-year averages for these environmental variables were used to analyze the influence of environmental factor on community diversity and stability.

## **2.2 | Biodiversity and functional trait composition**

For each of the 318 routes, we first measured species richness by the total number of species encountered in each route. We then calculated both community-weighted mean (CWM) and functional diversity (FD) of each individual trait or an aggregate metric which combines the four traits. To derive such an aggregate trait metric, we performed a principal component analysis (PCA) based on the four traits and obtained the first principal component, using the function in ‘FactoMineR’ for the R software (Lê, Josse, & Husson, 2008). The first principal

component (PC1) explained 56.3% of the total variation among the four traits (Figure S2), and its loadings on the four traits suggest a ‘fast-slow’ continuum in life history (Table S2). Specifically, a larger value of PC1 correspond to 'fast' species, characterized by smaller body size, shorter life span and nestling period, and larger clutch size, whereas a smaller value of PC1 correspond to ‘slow’ species, characterized by larger body size and longer life span and nestling period, and smaller clutch size.

For each individual trait or the aggregate trait (i.e. PC1), we calculated the corresponding CWM as the average of species trait values, weighted by their population abundance, and we calculated both abundance-weighted functional richness and functional evenness to represent FD among co-existing species, using the 'FD' package in the R software (Craven et al., 2018; Laliberté & Legendre, 2010). Functional richness captures the overall volume of multi-trait space, whereas functional evenness captures the uniformity of species trait distribution and is regarded as an indicator of interspecific niche complementarity (Ali, Lohbeck, & Yan, 2018; Mason, Mouillot, Lee, & Wilson, 2005). Because functional richness and evenness generated qualitatively similar results, we presented results of functional evenness in the main text and those of functional richness in the Supporting Information (Figure S6).

### 2.3 | Community stability

Total community biomass by route and year was calculated by summing species biomass across all species, where species biomass was derived as the product of species population size and average body mass. We then calculated the temporal stability of community biomass as the ratio of the temporal mean to the standard deviation (Tilman et al. 2006; Donohue et al., 2016; Wang et al., 2019):

$$ST_{\text{com}} = \frac{\sum_i \mu_i}{\sqrt{\sum_{i,j} w_{ij}}}$$

where  $\mu_i$  and  $w_{ii}$  represents the temporal mean and variance of the biomass of species  $i$ , respectively, and  $w_{ij}$  represents the temporal covariance between species  $i$  and  $j$ .

Mathematically,  $\mu_i = \frac{\sum_t B_{i,t}}{T}$ ,  $w_{ii} = \frac{\sum_t (B_{i,t} - \mu_i)^2}{T-1}$ , and  $w_{ij} = \frac{\sum_t (B_{i,t} - \mu_i)(B_{j,t} - \mu_j)}{T-1}$ , where  $B_{i,t}$  is the total biomass of species  $i$  in year  $t$ , and  $T$  is the number of years (i.e. 30). Theory clarified that the community stability could be partitioned into two multiplicative terms, i.e. average species stability ( $ST_{\text{pop}}$ ) and species asynchrony ( $\varphi$ ) (Thibaut & Connolly, 2013; Wang et al., 2019).  $ST_{\text{pop}}$  is calculated as the weighted average of species-level stability (Thibaut & Connolly 2013):

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$$ST_{\text{pop}} = \frac{\sum_i \mu_i}{\sum_i \sqrt{w_{ii}}}$$

Species asynchrony was defined as a community-wide measure to capture species compensatory dynamics:

$$\varphi = \frac{\sum_i \sqrt{w_{ii}}}{\sqrt{\sum_{i,j} w_{ij}}}$$

By definition,  $ST_{\text{com}} = ST_{\text{pop}} \cdot \varphi$ . Thus, species asynchrony provides a scaling factor connecting stability between species and community levels (Wang et al., 2019).

We noted that temporal trends in species and community biomass may influence the calculation of stability metrics (Lepš, Götzenberger, Valencia, & de Bello, 2019). Of the 318 routes, 40% had significant linear trends over the 30-year period studied. We thus calculated community stability using both original time series data and detrended ones by removing the linear trends of community biomass. These two metrics are highly correlated ( $r = 0.95$ ; Figure S3), so we presented only results based on the original data.

## 2.4 | Statistical analysis

We first examined the relative importance of  $ST_{\text{pop}}$  and  $\varphi$  in explaining the spatial variation of community stability using linear regressions and variance partitioning (Catano et al., 2020; Wilcox et al., 2017). We then investigated how biotic (species richness, FD, and CWMs) and environmental factors (temperature, precipitation, LAI) affect community stability ( $ST_{\text{com}}$ ) and its two components (i.e.  $ST_{\text{pop}}$  and  $\varphi$ ). For each biotic or environmental factor, we derived its effect sizes on each of the three stability metrics ( $ST_{\text{com}}$ ,  $ST_{\text{pop}}$  and  $\varphi$ ) using the standardized regression coefficient. While these effect size represented the overall influences of the respective factor on stability, we further developed a structural equation model (SEM) in light of Figure 1 to illuminate direct and indirect effects. We hypothesized that species richness and functional trait composition directly influenced the two components of community stability (i.e. species stability and species asynchrony), and all these metrics are regulated by environmental factors (Figure 1). In other words, environmental factors can affect avian community stability both directly and indirectly by shaping species richness and functional trait composition. We included only the CWM and FD of the aggregate ‘fast-slow’ trait metric (i.e. PC1; referred to as  $\text{CWM}_{\text{fast-slow}}$  and  $\text{FD}_{\text{fast-slow}}$ , respectively) to simplify the SEM and reduce the autocorrelation between exploratory variables. The SEM was fitted using the package 'piecewiseSEM' in R (Lefcheck, 2016).



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### 3 | RESULTS

$ST_{\text{com}}$  exhibited large spatial variation ranging from 0.7 to 5.8, which was explained by spatial variations in  $ST_{\text{pop}}$  and  $\varphi$  among routes (Figure 2a and 2b).  $ST_{\text{pop}}$  and  $\varphi$ , separately, each accounted for 26% and 34% of the variation in  $ST_{\text{com}}$ , and they together explained 40% (Figure 2c). From species to community levels, spatial asynchrony enhanced the temporal stability by on average 2.5 times (ranging from 1.2 to 4.6 times; Figure 2a and 2b).

We examined how spatial variations in  $ST_{\text{pop}}$  and  $\varphi$  might be explained by species richness, functional trait composition, and environmental factors (Figure 3).  $ST_{\text{pop}}$  was positively related to species richness and the CWM of clutch size, and it was negatively related to the CWM and FD of body size and nestling period and the FD of clutch size.  $\varphi$  exhibited no significant relationship with species richness or the FD of any trait, but it was negatively related to the CWM of all traits except clutch size. Combined,  $\text{CWM}_{\text{fast-slow}}$  was negatively related to both  $ST_{\text{pop}}$  and  $\varphi$ , explaining 7% and 11% of their variation, respectively. These were much higher than those explained by species richness or  $\text{FD}_{\text{fast-slow}}$  ( $r^2 = 0.0002\sim 0.05$ ). At the community level,  $ST_{\text{com}}$  was not related to species richness, but it was positively related to both  $\text{CWM}_{\text{fast-slow}}$  and  $\text{FD}_{\text{fast-slow}}$ . Moreover,  $ST_{\text{pop}}$  was positively related to temperature, precipitation, and LAI, whereas  $\varphi$  was positively related to temperature only. As a result,  $ST_{\text{com}}$  exhibited positive relations with temperature and precipitation (Figure 3).

Our SEM confirmed the negative associations between  $\text{CWM}_{\text{fast-slow}}$  and  $ST_{\text{pop}}$  or  $\varphi$  (Figure 4a). But in contrast to bivariate relationships,  $\text{FD}_{\text{fast-slow}}$  was positively associated with  $\varphi$  but not related to  $ST_{\text{pop}}$ , and species richness was not related to either  $ST_{\text{pop}}$  or  $\varphi$ . Moreover, SEM separated direct and indirect effects of environmental variables (Figure 4a). Temperature had positive direct effects on both  $ST_{\text{pop}}$  and  $\varphi$ , and it had a positive indirect effect on  $\varphi$  through increasing  $\text{FD}_{\text{fast-slow}}$ . These direct and indirect pathways led to positive net effects of temperature on  $ST_{\text{pop}}$ . Precipitation had a weak indirect negative effect on  $\varphi$  by decreasing  $\text{FD}_{\text{fast-slow}}$ . LAI exhibited positive associations with species richness and negative ones with  $\text{CWM}_{\text{fast-slow}}$  and  $\text{FD}_{\text{fast-slow}}$ , which resulted in multiple compound pathways with either positive or negative effects on  $ST_{\text{pop}}$  and  $\varphi$ . All combined, LAI had net positive effects on both  $ST_{\text{pop}}$  and  $\varphi$ , resulting in a net positive effect on  $ST_{\text{com}}$ . Taken together,  $\text{CWM}_{\text{fast-slow}}$  and temperature are the most important biotic and environmental factor, respectively, in driving avian community stability (Figure 4b).

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## 4 | DISCUSSION

### 4.1 | 'Fast-slow' trait composition drives avian community stability

Our analyses showed that avian community stability was mainly driven by the community-weighted mean (CWM) of the 'fast-slow' trait, and only moderately by species richness and functional diversity (FD). Communities dominated by 'fast' species were more stable, due to both higher average species stability and higher species asynchrony. This result remains highly consistent regardless of whether individual functional traits or the aggregate 'fast-slow' trait (i.e. PC1) were used. In communities dominated by 'fast' species, the higher average species stability can be attributed to the higher resilience and recovery rate of 'fast' species, despite their lower resistance under environmental stress (Pribil & Houlahan, 2003; Turvey, Green, & Holdaway, 2005; Werner & Griebeler, 2012). Moreover, the 'fast' species, characterized by small body size and large clutch size, can have large population sizes and thus undergo lower temporal fluctuations due to demographic stochasticity (De Mazancourt et al., 2013; Peltonen & Hanski, 1991; Tilman et al., 1997). In contrast, the 'slow' species tend to have population size and thus are likely to be influenced by demographic stochasticity. We also found that communities dominated by 'fast' species exhibited higher species asynchrony. This may be because an increased dominance of 'fast' species (with small body size and biomass) results in a higher evenness in species biomass distribution, which in turn increases species asynchrony (Loreau & de Mazancourt, 2008; Thibaut & Connolly, 2013).

Compared with the CWM of the 'fast-slow' trait, species richness and functional diversity were found to have much weaker effects on community stability (Figure 4). Our SEM suggested that functional diversity of the 'fast-slow' trait had a positive effect on community stability by increasing species asynchrony. A higher functional diversity in 'fast-slow' traits indicates more diverse life-history strategies and capacities to cope with disturbances, which lead to higher asynchrony between species. We note, however, that bivariate analyses revealed no relationship between functional diversity and species asynchrony, which was likely due to the negative association between functional diversity and CWM and the fact that CWM was positively related to species asynchrony (Figure 4). Species richness also had an overall stabilizing effects on avian communities through increasing species stability. Theory predicts either positive or negative effects of biodiversity on species stability (Thibaut & Connolly, 2013; Tilman, 1999; Houlahan et al. 2018). While grassland experiments reported negative effects of species richness on species stability (Hector et al., 2010; Tilman et al., 2006), our analysis with bird populations revealed a positive effect of species richness on species biomass stability, consistent with prior studies

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on the stability of species population size (Mikkelsen et al. 2011). Such a positive association could be explained by the fact that more diverse communities include a higher proportion of ‘fast’ species.

Taken together, our results are in line with the general hypothesis that ‘fast-slow’ traits have important roles in species and community stability (Craven et al., 2018). That said, our findings differ from recent studies on grasslands in two respects. First, while our analyses identified the CWM of ‘fast-slow’ traits as the major driver of community stability, studies on grasslands found that the functional diversity of ‘fast-slow’ traits was more important for maintaining community stability than CWM (Craven et al. 2018). Second, while our study showed that communities dominated by ‘fast’ species were more stable, grassland communities dominated by ‘fast’ species were shown to exhibit lower stability than those dominated by ‘slow’ species (Craven et al. 2018). In both our study (Figures S4 & S5) and the recent study on grasslands (Craven et al. 2018), the mean and standard deviation of community biomass both decreased with the CWM of the ‘fast-slow’ trait. However, in our data, the stabilizing effect of the CWM of the ‘fast-slow’ trait by decreasing the standard deviation was much stronger than the destabilizing effect through decreasing the mean (Figure S5), which leads to an overall stabilizing effect. One possible explanation for these contrasting results is that our analysis used bird population records for a much longer time period (30 years) than did the grassland study (mostly  $\leq 4$  years, with a few exception of  $> 10$  years). Longer records allow better opportunities for detecting recovery processes (i.e. resilience) that are driven by ‘fast’ traits, whereas shorter records may better capture immediate responses to disturbances (i.e. resistance) that are driven by ‘slow’ traits.

#### **4.2 | Environmental control over avian community stability**

Our SEM revealed both direct and indirect effects of environmental factors on avian community stability. Of the three environmental factors (i.e. temperature, precipitation, and LAI), only temperature exhibited direct, positive associations with species stability and asynchrony. Warmer regions tend towards greater temporal stability in the climate (Terando, Easterling, Keller, & Easterling, 2012) and thus have more stable species dynamics. In addition, migratory species in colder areas experience higher population fluctuations due to migration-induced deaths and the influences of climate changes (Gilroy, Gill, Butchart, Jones, & Franco, 2016; Lameris et al., 2017; Morrison, Robinson, Clark, Risely, & Gill, 2013), which decreases species stability and increases the synchrony among species.

All three environmental factors influence species richness and functional trait composition and thus have indirect effects on community stability. That said, because species

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richness and the functional diversity exert relatively weak effects on community stability, the indirect effects of environmental factors through species richness and functional diversity are also weak. The CWM of ‘fast-slow’ trait decreased as the LAI increased, suggesting a higher proportion of ‘fast’ species in more productive regions. This can be understood from associations between bird species traits and habitat preferences. Higher LAI indicates a more closed canopy vegetation such as dense forest, which are suitable for small-bodied ‘fast’ bird species. In contrast, lower LAI indicates more open habitats such as wetlands, estuaries, bushes, and bare mountain cliffs (Colombo, Bellingeri, Fasolini, & Marino, 2003; Majasalmi & Rautiainen, 2020), which are preferred by large-bodied and long-lived ‘slow’ species such as waterfowls and raptors. Through its positive relation with the ‘fast’ trait, ecosystem productivity (LAI) contributes to increasing community stability.

### **4.3 | Implications and limitations**

The results reported here have implications for understanding functional consequences of bird population changes. Rosenberg et al., (2019) detected a continental-scale population decline of North American birds since 1970s. Their analysis suggested that ‘fast’, small species suffered greater declines, e.g. Old World sparrows (-81.1%), blackbirds (-44.2%), American sparrows (-38%), and wood warblers (-37.6%), whereas ‘slow’, large species experienced less pronounced declines or even increased, e.g. turkeys and grouses (+25%), waterfowls (+56%), raptors (+200%), and cranes (+914.5%) (Figure S7). Such asymmetric population changes alter the community trait composition and lead to an increased proportion of ‘slow’ traits (Figure 5a). In light of our results, such an increased proportion of ‘slow’ traits could lead a reduced community stability over time. Our preliminary analysis supports such a prediction: following the population decrease of ‘fast’ species and population increase of ‘slow’ species, avian community stability generally decreased during the past three decades (Figure 5b). Thus, ecosystem management efforts that alleviates population decline of ‘fast’ bird species are important for maintaining stability at the community level.

We make two caveats in the interpretation of our results. First, as our study is motivated from the fundamental angle to explore the biotic drivers of community stability at a continental scale using a less studied taxon (i.e. birds), we have focused on stability of total community biomass, rather than that of individual species abundances. The latter might be more relevant to conservation practices targeting at the preservation of particular species. Expanding the implications of our analyses for biodiversity conservation requires redefinition and measurement of ‘success’ in terms of the entire ecosystem or bird habitat sustainability. Second, our data cover large spatial and temporal extents and are likely to contain

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observational error, particularly for large-bodied species with lower population size but larger home ranges. Such observational errors may account, to some extent, for the lower stability for slow species, in addition to our interpretation based on their low resilience and high demographic stochasticity. Previous studies showed that observational errors can explain a considerable amount of variation in community stability (de Mazancourt et al., 2013). Such observational errors may similarly affect the quantification of bird community stability in this study, but one cannot assess its contribution based on the current data. A rigorous estimation of the detectability and its impact on the quantification of species and community stability would require improved sampling designs using local routes as a pilot experiment (Newson, et al., 2008).

## 5 | CONCLUSIONS

Understanding the biotic and abiotic drivers underlying the stability of avian communities is important for predicting their responses to global changes. Our study demonstrates that ‘fast-slow’ trait composition is a major driver of avian community stability. Temperature is the most significant abiotic driver of community stability, but its effect is weak compared to that of ‘fast-slow’ trait composition. By investigating avian community stability over large spatial scales and along environmental gradients, our study adds to the diversity-stability research that have so far largely focused on plant and aquatic ecosystems at small scales and under fixed environmental conditions (Cardinale et al., 2012; Gonzalez et al. 2020). Importantly, in line with the growing body of literature emphasizing the functional implications of ‘fast-slow’ trait continuum, our study demonstrates the importance of ‘fast-slow’ trait composition in understanding the stability of bird species and communities. In addition, the positive relationship between community stability and temperature in our data suggests that future warming may enhance the stability of avian communities. Taken together, an integrated framework combining community trait composition and temperature is needed to understand the responses of bird communities in a changing environment.

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### **SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

### **ACKNOWLEDGEMENTS**

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### **CONFLICT OF INTEREST STATEMENT**

All authors declare that there is no conflict of interest.

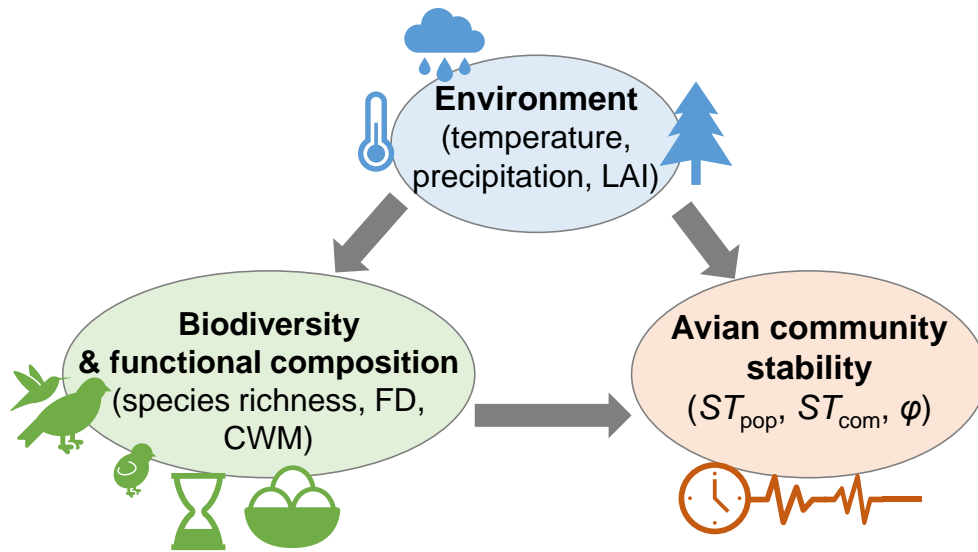
### **AUTHORS' CONTRIBUTIONS**

Shaopeng Wang and Zhouyuan Li conceived the idea and designed methodology; Zhouyuan Li and Heng Zhang collected the data; Zhouyuan Li, Heng Zhang, Shaopeng Wang, and Yanjie Xu analysed the data; Zhouyuan Li and Shaopeng Wang led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

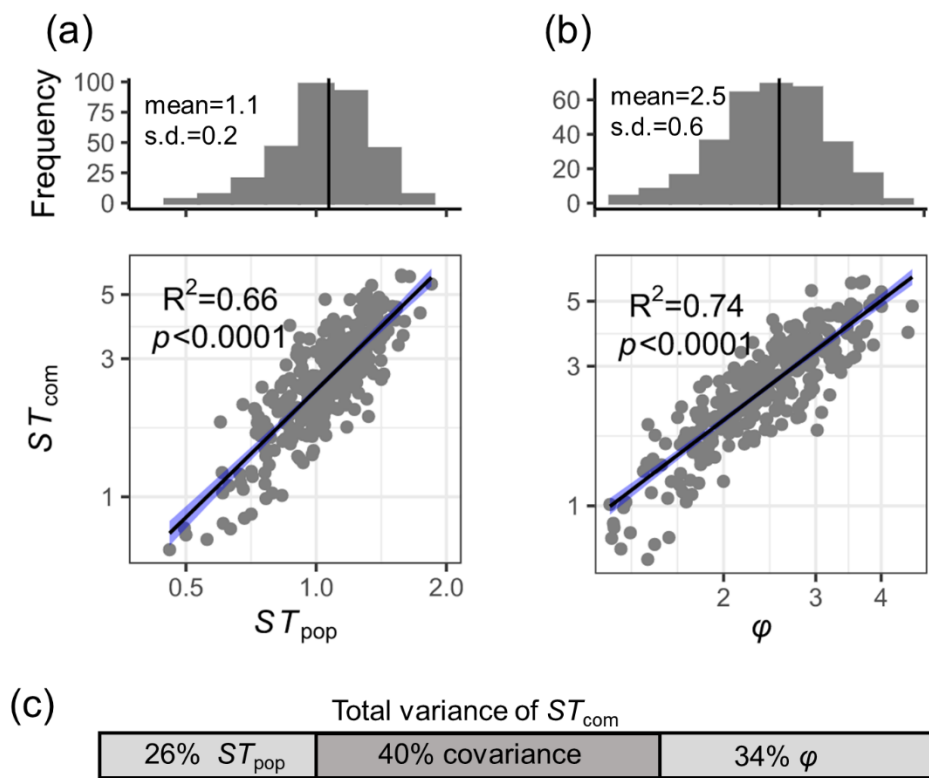
### **DATA ACCESSIBILITY**

Data can be accessed through the North American Breeding Bird Survey (<https://www.pwrc.usgs.gov/BBS/RawData/>), traits (<https://dx.doi.org/10.6084/m9.figshare.c.3306933>), and environment (<http://iridl.ldeo.columbia.edu/>; <http://mpimet.mpg.de/cdi>; <http://www.geodata.cn/thematicView/GLASS.html>)

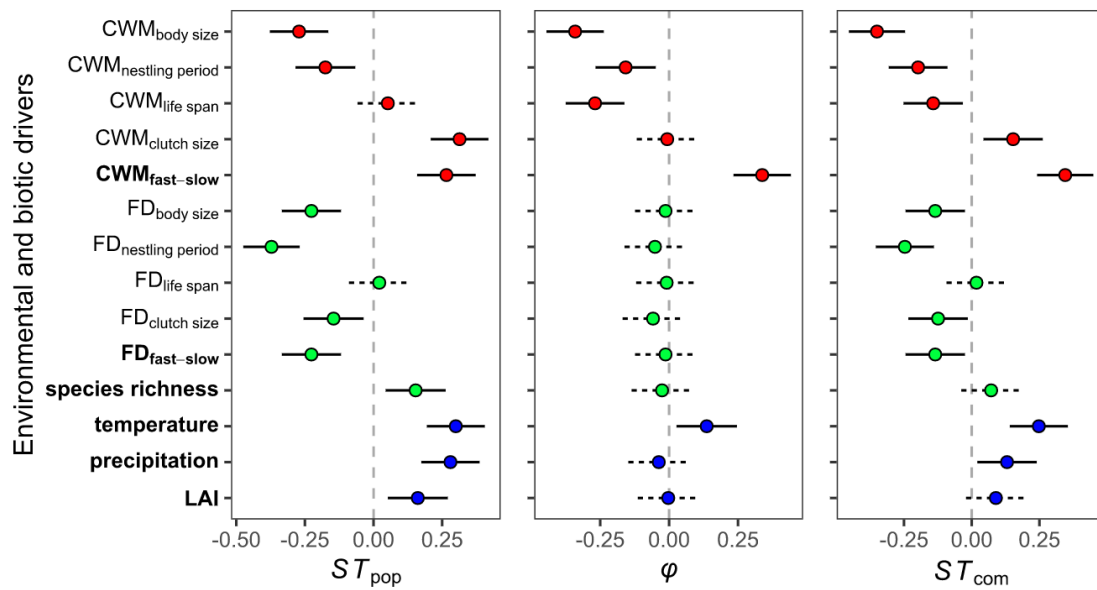
## FIGURES



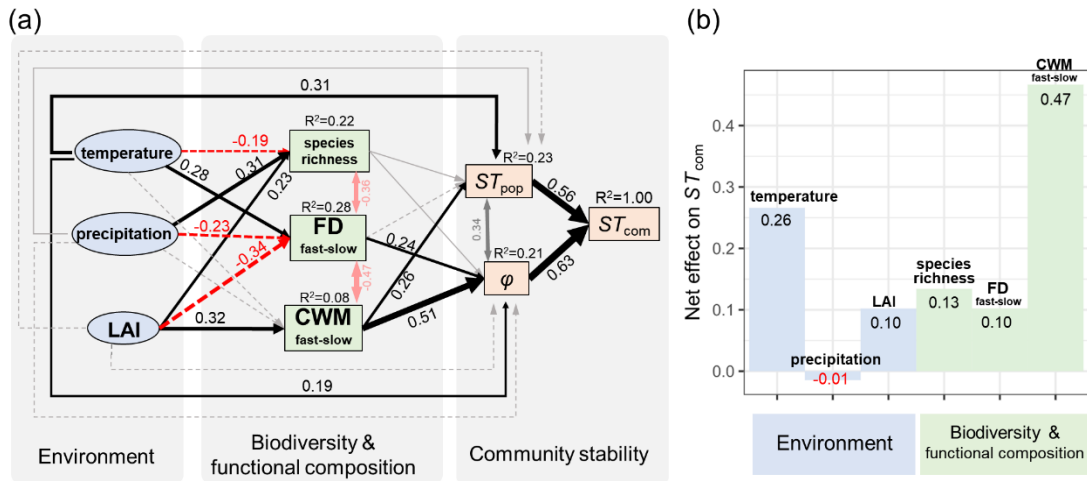
**FIGURE 1** The conceptual framework to examine the effects of species richness and trait composition on avian community stability along environmental gradients. Variables in the parentheses represent the metrics used in our analysis: FD = functional diversity, CWM = community weighted mean of functional trait; LAI = leaf area index,  $ST_{com}$  = community stability,  $ST_{pop}$  = species stability,  $\phi$  = species asynchrony.



**FIGURE 2** Relationships between avian community stability ( $ST_{com}$ ) and species-level stability ( $ST_{pop}$ ) (a) and species asynchrony ( $\phi$ ) (b), with the frequency distribution of  $ST_{pop}$  and  $\phi$ , across 318 sites of North America. The black lines indicate linear regressions on a log-log scale. (c) shows the variance partitioning result for  $ST_{com}$ .

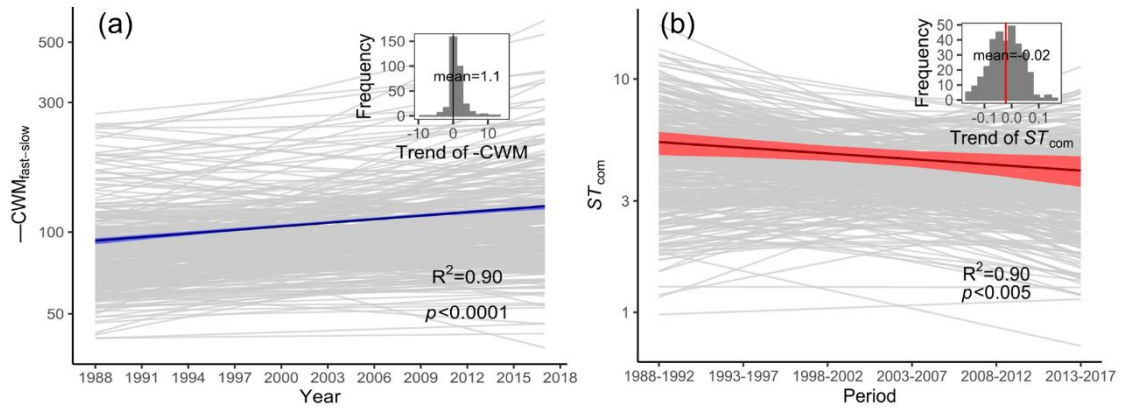


**FIGURE 3** Effect sizes of functional trait (CWM = community-weighted mean and FD=functional diversity), species richness, and environmental variables on the stability metrics ( $ST_{pop}$  = species-level stability;  $\phi$  = species asynchrony;  $ST_{com}$  = community-level stability). The effect size was calculated as the standardized regression coefficient. The solid and dashed bars represent significant ( $p < 0.05$ ) and non-significant ( $p > 0.05$ ) relationships, respectively. Variables in bold are used in the SEM in Figure 4.



**FIGURE 4** Structural equation model (SEM) depicting the relationships between the environment, trait composition and species richness, and community stability (a). Overall, the model fits the data well: Fisher's C = 15.71, AIC= 85.713, and  $p$  value = 0.33. The solid and dashed arrows represent positive and negative relationships, respectively, and the light-grey arrows represent non-significant relationships ( $p > 0.05$ ). The net effects of different environmental and biotic factors on community stability were shown in (b).





**FIGURE 5** The temporal trend of community weighted mean (CWM) of ‘fast-slow’ traits (a) and community stability ( $ST_{com}$ ) (b) across the 318 sites of North America. For the community stability, we calculated the temporal stability of community biomass for six 5-year windows (i.e. 1988-1992, 1993-1997, etc.), and the trends are derived from these six stability values. Each gray line represents the temporal trend for a local sampling route, and black and red bold lines represent the overall trends (using mixed-effects models with sampling routes as the random effect).