

[Resilience of Avian Communities to](https://www.frontiersin.org/articles/10.3389/fcosc.2022.918873/full) [Urbanization and Climate Change:](https://www.frontiersin.org/articles/10.3389/fcosc.2022.918873/full) [an Integrative Review](https://www.frontiersin.org/articles/10.3389/fcosc.2022.918873/full)

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Specialty section:

This article was submitted to Global Biodiversity Threats, a section of the journal Frontiers in Conservation Science

> Received: 12 April 2022 Accepted: 20 June 2022 Published: 12 July 2022

Citation:

McCloy MWD, Andringa RK and Grace JK (2022) Resilience of Avian Communities to Urbanization and Climate Change: an Integrative Review. Front. Conserv. Sci. 3:918873. [doi: 10.3389/fcosc.2022.918873](https://doi.org/10.3389/fcosc.2022.918873)

The concept of ecological resilience is widely used to assess how species and ecosystems respond to external stressors but is applied infrequently at the level of the community or to chronic, ongoing disturbances. In this review, we first discuss the concept of ecological resilience and methods for quantifying resilience in ecological studies. We then synthesize existing evidence for the resilience of avian communities to climate change and urbanization, two chronic disturbances that are driving global biodiversity loss, and conclude with recommendations for future directions. We only briefly discuss the theoretical framework behind ecological resilience and species-specific responses to these two major disturbances, because numerous reviews already exist on these topics. Current research suggests strong heterogeneity in the responses and resilience of bird communities to urbanization and climate change, although community disassembly and reassembly is high following both disturbances. To advance our understanding of community resilience to these disturbances, we recommend five areas of future study (1) the development of a standardized, comprehensive community resilience index that incorporates both adaptive capacity and measures of functional diversity, (2) measurement/modeling of both community resistance and recovery in response to disturbance, (3) multi-scale and/or multi-taxa studies that include threeway interactions between plants, animals, and climate, (4) studies that incorporate interactions between disturbances, and (5) increased understanding of interactions between ecological resilience and socio-ecological dynamics. Advancement in these areas will enhance our ability to predict and respond to the rapidly accelerating effects of climate change and urbanization.

Keywords: bird, adaptive capacity, vulnerability, biodiversity, conservation, resistance, recovery, land use change

1 INTRODUCTION

1.1 Overview

A major conservation priority in the field of modern ecology is predicting and ameliorating the effects of climate change and their synergistic interactions with land-use change [\(Jetz et al.,](#page-14-0) [2007;](#page-14-0) [Northrup et al., 2019\)](#page-15-0), particularly in regions of high biological diversity and/or endemism [\(Myers et al., 2000](#page-15-0)). To effectively address this priority, it is critical for scientists and conservation practitioners to have a thorough understanding of: (1) the current manifestation and projected future effects of major anthropogenic factors on ecosystems and natural communities, and (2) methods of quantifying and conceptually understanding how ecosystems, communities, and populations are responding to these changes. Ecological resilience [\(Holling,](#page-13-0) [1973\)](#page-13-0) is the ability of a system to resist ([Karp et al., 2011](#page-14-0); [Scheffer](#page-15-0) [et al., 2015\)](#page-15-0), and recover from [\(Harrison, 1979](#page-13-0); [Selwood et al.,](#page-16-0) [2015\)](#page-16-0) perturbations, thus encompassing both the process of resistance, the magnitude of disturbance that causes a change in structure, and recovery, the speed of return to the original community function (Table 1) [\(Tilman and Downing, 1994](#page-16-0); Côté [and Darling, 2010](#page-13-0)). Ecological resilience provides a framework for quantifying and conceptualizing ecological response to anthropogenic change at multiple ecological scales ([Allen et al., 2005](#page-12-0)), but reviews at the level of the ecological community are lacking.

Here, we synthesize existing literature on the topic of ecological resilience in birds, and examine how it can be more effectively applied at the level of the community, especially regarding chronic disturbance. Additionally, we discuss how further integration of the concept of resilience with other conservation-oriented frameworks (i.e., adaptive capacity and vulnerability) can improve conservation assessments. Bird communities provide excellent case studies for ecological resilience because they are well-studied, perform a diverse array of ecological functions, and are important providers of ecosystem services [\(Sekercioglu, 2006](#page-15-0); [Bregman et al., 2016\)](#page-12-0). Birds are also conspicuous to the general public, leading to an

abundance of community science data that can be paired with climate and land-use data to assess the effects of these drivers on avian populations and community structure [\(Neate-Clegg et al.,](#page-15-0) [2020;](#page-15-0) [Binley et al., 2021\)](#page-12-0). Because birds occupy a range of ecological functions ([Sekercioglu, 2006\)](#page-15-0), their community-level resilience may be indicative of ecosystem resilience [\(Fischer et al.,](#page-13-0) [2007](#page-13-0)); and birds drive conservation efforts in many regions, particularly in biodiversity hotspots [\(Myers et al., 2000](#page-15-0); [Larsen](#page-14-0) [et al., 2012\)](#page-14-0).

Resilience can be defined as the capacity of a community to absorb and recover from disturbance without affecting the function and stability of the community or broader ecosystem (Table 1) ([Ives and Carpenter, 2007;](#page-13-0) Côté [and Darling, 2010\)](#page-13-0). This is consistent with the working definition adopted by the majority of recent (post-2015) ecological literature ([Fremier](#page-13-0) [et al., 2015](#page-13-0); [Scheffer et al., 2015;](#page-15-0) [Levine et al., 2016;](#page-14-0) [Falk et al.,](#page-13-0) [2019;](#page-13-0) [Morelli et al., 2020\)](#page-15-0). When community resistance is overcome, community disassembly, or nonrandom loss of species from within a community, can occur [\(Zavaleta et al.,](#page-16-0) [2009](#page-16-0)). Following disassembly, recovery does not necessitate a return to the original community composition and structure. Instead, recovery can involve turnover of species within a community (i.e., community reassembly, Table 1; [Schaefer](#page-15-0) [et al., 2008\)](#page-15-0) that leads to a resumption of original community functionality. [Figure 1](#page-2-0) illustrates the resilience of a community to climate change and urbanization through a variety of different mechanisms and outcomes.

In this review we focus on avian community resilience in response to the independent and interactive effects of climate change and urbanization, two chronic anthropogenic drivers of global biodiversity loss and community disassembly ([Travis,](#page-16-0) [2003;](#page-16-0) [Jetz et al., 2007](#page-14-0); [Kampichler et al., 2012](#page-14-0); [Yalcin and](#page-16-0) [Leroux, 2018](#page-16-0)). Resilience is typically measured following acute disturbances, where recovery can be easily observed. However, both acute and chronic disturbances have the capacity to shape ecological communities ([May, 1977;](#page-14-0) [Johnstone et al., 2016\)](#page-14-0) and many chronic disturbances, such as climate change and urbanization, drive global conservation priorities. An

abundance of published literature exists around the broad topics of avian responses to climate change and urbanization, and numerous reviews have synthesized various aspects ranging from species-specific responses (e.g., [Marzluff and Ewing, 2008](#page-14-0); [Reif, 2013;](#page-15-0) [Scridel et al., 2018\)](#page-15-0), to ecosystem-level effects ([Garrett](#page-13-0) [et al., 2006](#page-13-0); [Doney et al., 2012](#page-13-0); [Aronson et al., 2014](#page-12-0)), to economic effects ([Tol, 2009\)](#page-16-0), among others. We only briefly discuss the theoretical framework behind ecological resilience and speciesspecific responses to urbanization and climate change, because numerous thorough reviews of these topics already exist (e.g., [Holling, 1973;](#page-13-0) [Gunderson, 2000](#page-13-0); [Crick, 2004](#page-13-0); [Chace and Walsh,](#page-12-0) [2006;](#page-12-0) [Jiguet et al., 2006;](#page-14-0) [Leech and Crick, 2007;](#page-14-0) [Bonier, 2012](#page-12-0); [Reif, 2013](#page-15-0); [Scheffer et al., 2015](#page-15-0); [Seress and Liker, 2015](#page-16-0); [Scridel](#page-15-0) [et al., 2018;](#page-15-0) [Falk et al., 2019](#page-13-0); [Maxwell et al., 2019](#page-14-0)). Instead, we synthesize current literature that apply the concept of ecological resilience to avian responses to climate change and urbanization at the community level, and provide recommendations for future studies, including improved methods for quantifying resilience across ecosystem scales.

1.2 Quantifying Resilience

Empirical methods for quantifying resilience in avian communities range from species-specific measures to functional diversity indices, with associated trade-offs in ease of calculation, efficacy, complexity, and relevance ([Fischer et al.,](#page-13-0) [2007\)](#page-13-0). Species abundance, occupancy probability, richness, and diversity (e.g., Shannon Index) have been widely used as straightforward proxies for resilience [\(Clergeau et al., 1998](#page-12-0); [Johnson and Winker, 2010](#page-14-0); [Irizarry et al., 2021](#page-13-0)). For example, [Selwood et al. \(2015\)](#page-16-0) used species occupancy data generated by community scientists in BirdLife Australia's Atlas Program to

estimate resistance and recovery of Australian birds following a 13-year drought. Abundance, occupancy, richness, and diversity are popular methods for estimating resilience because they are easy to calculate and are adequate for analyzing localized resistance and recovery of species, guilds, or communities [\(Johnson and Winker, 2010;](#page-14-0) [Karp et al., 2011](#page-14-0); [Selwood et al.,](#page-16-0) [2015](#page-16-0); [Irizarry et al., 2021](#page-13-0)). However, these metrics alone convey little information regarding niche overlap or redundancy, which are important aspects of community resilience. They also do not account for temporal and spatial heterogeneity in the niche space, which may change as a community undergoes a chronic disturbance. Thus, they provide an incomplete (and in some cases, misleading) picture of community resilience, especially at broader temporal or spatial scales.

At the community level, functional diversity indices ([Table 1](#page-1-0)) offer a more complex picture of community resilience ([Allen](#page-12-0) [et al., 2005;](#page-12-0) [Mason et al., 2005](#page-14-0); [Ricotta et al., 2014](#page-15-0); [Morelli et al.,](#page-15-0) [2020](#page-15-0)), and are frequently used in assessments of ecosystem services [\(Sekercioglu, 2012;](#page-15-0) [Lavorel et al., 2013](#page-14-0); [Song et al.,](#page-16-0) [2014](#page-16-0)). In contrast to species diversity, functional diversity is concerned with the range of functional traits of species within a community, or those components of the phenotype that influence ecosystem functioning [\(Petchey and Gaston, 2006\)](#page-15-0) and is calculated using functional groups, or groupings of species based on similarity in ecological functions [\(Blondel,](#page-12-0) [2003](#page-12-0)), as opposed to taxonomic groups ([Hooper et al., 2005\)](#page-13-0). Functional diversity indices can be broadly grouped into those that describe how much of the functional niche space is filled by species in the community (i.e., functional richness), or how that space is filled (i.e., functional evenness, functional divergence/ variance) ([Schleuter et al., 2010](#page-15-0)). Thus, functional diversity

FIGURE 1 | Influence diagram representing community resilience, via the mechanisms by which different community-level outcomes may result from the chronic disturbances of climate change and urbanization, and their interactions. In this diagram, resistance is depicted through the breadth of disturbance and the underlying mechanisms of community response, while recovery occurs through community reassembly and/or when a given community reaches a state of equilibrium. Resistance is a buffer against disturbance that allows for community persistence until it is overcome by the breadth of disturbance. Mechanisms such as adaptive capacity, functional diversity, and biogeography can contribute to resistance and/or recovery by returning a community to its pre-disturbance state when resistance is overcome (illustrated by dotted arrows). This diagram is not a comprehensive illustration of mechanisms and outcomes, but instead depicts those that are commonly associated with climate change and urbanization. These outcomes are also not finite, climate change and urbanization will continue to operate on reassembled and alternative communities through these mechanisms, producing later community disassembly, reassembly, and alternative stable states (Created with BioRender.com).

indices consider redundancy and complementarity of species within a community [\(Schleuter et al., 2010](#page-15-0)) and provide insights to ecosystem functions ([Bremner et al., 2003;](#page-12-0) [Mason et al., 2005\)](#page-14-0), but may not respond to disturbance in the same way as species diversity [\(Lee and Martin, 2017\)](#page-14-0). Functional diversity indices may act as indicators of community resilience, with higher diversity correlating with higher resilience ([Allen et al., 2005](#page-12-0)).

Functional evenness is a functional diversity index that has garnered particular attention in the resilience literature. It represents the distribution of species abundances across functional space (Villé[ger et al., 2008](#page-16-0)), providing an indication of functional redundancies of species within a community and thus the capacity for a community to sustain species loss without suffering declines in function ([Morelli et al., 2020](#page-15-0)). This metric has found wide application in quantifying community responses to disturbance, such as studying how avian communities are responding to forest change in the Amazon ([Bregman et al., 2016\)](#page-12-0) and how plant communities respond to various types of disturbance [\(Fontaine](#page-13-0) [et al., 2006](#page-13-0); [Biswas and Mallik, 2010](#page-12-0); [Schneider et al., 2017\)](#page-15-0). However, measuring functional evenness has proven to be difficult since the traditional FEve Index (Villé[ger et al., 2008\)](#page-16-0) is problematic for detecting community composition in cases where multiple species occupy the same functional space [\(Mouchet et al.,](#page-15-0) [2010;](#page-15-0) [Ricotta et al., 2014;](#page-15-0) [Van der Linden et al., 2016](#page-16-0)). Despite these technical issues, functional evenness and other diversity indices are the preferred measures of resilience over phylogenetically-focused metrics because of their emphasis on ecosystem and community functions, and should be used in place of, or in conjunction with these when possible ([Mouchet et al., 2010](#page-15-0)).

1.3 Adaptive Capacity and Resilience

Adaptive capacity is the ability of a system to cope with or adjust to changes in external circumstances or internal demands [\(Smit et al.,](#page-16-0) [2001](#page-16-0); [Carpenter and Brock, 2008](#page-12-0); [Engle, 2011](#page-13-0); [Thurman et al.,](#page-16-0) [2020](#page-16-0)), and is a central deterministic component of resilience that affects both resistance and recovery ([Gallopin, 2006;](#page-13-0) [Carpenter](#page-12-0) [and Brock, 2008\)](#page-12-0). Although adaptive capacity can be applied to entire ecosystems [\(Angeler et al., 2019](#page-12-0)), ecological adaptive capacity is most often applied at the species level. There are three generally recognized components of adaptive capacity: phenotypic plasticity, dispersal ability, and genetic diversity ([Beever et al., 2016](#page-12-0)). These components can be further divided into individual attributes and life history traits, which allows researchers, policymakers, and practitioners to easily calculate the adaptive capacity of individual species [\(Thurman et al.,](#page-16-0) [2020\)](#page-16-0). At the community-level, adaptive capacity can be estimated for communities indirectly by generalizing from the adaptive capacity of multiple species within that community ([Nicotra et al., 2015;](#page-15-0) [Siders, 2019](#page-16-0); [Thurman et al., 2020](#page-16-0)), or from representative species from different functional groups ([Thurman et al., 2020\)](#page-16-0). For example, if many species within a community have a low adaptive capacity, then that community as a whole may be assumed to also have a low adaptive capacity.

Adaptive capacity is a critical component of resilience ([Gallopin,](#page-13-0) [2006](#page-13-0); [Carpenter and Brock, 2008](#page-12-0)), however, there remains a disconnect between the application of adaptive capacity at the species level and the resilience of entire ecological communities

(subsequently referred to simply as, "communities"). We suggest that these concepts be considered together in a systems-based approach to analyzing community dynamics in the face of global change. Community ecologists may benefit from looking at the sociological literature, for which adaptive capacity is often used to calculate resilience of human populations [\(Smit and Wandel, 2006\)](#page-16-0). These methods may be transferable to some extent to ecological communities, although the specific mechanisms driving adaptive capacity and resilience in human systems often differ from those of ecological systems [\(Thurman et al., 2020\)](#page-16-0). For example, the resilience of human communities can be calculated by averaging the adaptive capacity of individual households for various indicators, then adding additional community-level features (e.g., community organization, dependence on resources) [\(Maldonado](#page-14-0) [and Moreno-Sanchez, 2014\)](#page-14-0). In an analogous manner, an index for resilience of ecological communities could include the average adaptive capacities of species within the community (weighted, for example, by relative abundance or biomass), and communitylevel metrics such as functional diversity. However, assessing the determinants of adaptive capacity across multiple species can be difficult [\(Siders, 2019](#page-16-0)) and consensus is needed on community traits influencing resilience, including and in addition to measures of functional diversity. The ability to assess and quantify adaptive capacity across avian communities will therefore greatly aid in understanding the interplay between adaptive capacity and avian resilience in the face of urbanization and climate change.

2 URBANIZATION AND AVIAN COMMUNITY RESILIENCE

As the global human population grows, widespread losses of habitat and biodiversity are increasingly attributed to urbanization and land use change- in particular, conversion to agriculture. Here we focus on urbanization instead of agricultural conversion because of the rapid growth of urban land area. By 2030, urban land area is projected to increase by around 1.5 million square km, worldwide ([Seto et al., 2011;](#page-16-0) [Seto et al., 2012\)](#page-16-0) with 70% of the global human population predicted to live in urban areas by 2050 ([Seto et al., 2011](#page-16-0)). This urban land conversion is occurring at the highest rates in global biodiversity hotspots [\(Seto et al., 2012\)](#page-16-0), which provide critical avian habitat. Here, we focus on avian community-level responses to urbanization and not species-specific responses because other reviews already exist on these topics (e.g., [Chace](#page-12-0) [and Walsh, 2006;](#page-12-0) [Bonier, 2012](#page-12-0); [Seress and Liker, 2015](#page-16-0)). We discuss the impacts of urban conversion on avian communities and the subsequent effects on community resilience.

2.1 Impacts of Urban Conversion on Avian Communities

2.1.1 Intermediate Disturbance and Ecosystem Stress-Gradient Hypotheses

Urbanization is widely considered to be a primary driver of biodiversity loss, biotic and seasonal homogenization ([McKinney, 2006;](#page-14-0) [Leveau et al., 2021](#page-14-0)), and community

disassembly and destabilization, particularly for specialist species ([Biamonte et al., 2011](#page-12-0)). There are two primary hypotheses that predict the response of avian communities to urbanization: the intermediate disturbance hypothesis and the ecosystem stressgradient hypothesis. Both of these predictive hypotheses provide insights to how avian communities respond to disturbance events in terms of diversity and richness, and therefore may help predict their resilience and adaptive capacity. Under the intermediate disturbance hypothesis, communities are expected to be more functionally diverse and speciose when disturbance is at an intermediate level, neither too rare nor too common ([Grimes, 1973](#page-13-0); [Horn, 1975](#page-13-0); [Connell, 1978\)](#page-12-0). This hypothesis is typically applied over a temporal scale, but within the context of urbanization it is often examined along a spatial scale, with intermediate urbanization conditions (e.g., suburban habitats, urban habitats with green spaces, etc.) predicted to be more diverse, and thus resilient, than low or high levels of urbanization. In contrast to the intermediate disturbance hypothesis, the ecosystem stress-gradient hypothesis predicts a decrease in resilience, as measured by species richness and/or functional diversity, as stress increases within a habitat [\(Bertness](#page-12-0) [and Callaway, 1994\)](#page-12-0). Within the context of urbanization, this hypothesis predicts that richness and diversity will be highest in non-urban, intact habitats and lowest in urban habitats [\(Lepczyk](#page-14-0) [et al., 2008;](#page-14-0) [Tomasevic, 2017;](#page-16-0) [Evans et al., 2018](#page-13-0)).

The ecosystem stress-gradient hypothesis is widely supported by the literature on avian diversity, with diversity (and thus, resilience) steadily declining as urbanization increases ([McKinney, 2008](#page-14-0)). However, the intermediate disturbance hypothesis has also found support from studies examining species richness (another measure of resilience), with richness highest at intermediate levels of urbanization [\(Blair, 1996](#page-12-0); [Marzluff, 2001](#page-14-0); [Leveau and Leveau, 2005](#page-14-0); and [Lepczyk et al.,](#page-14-0) [2008\)](#page-14-0). For example, in the early stages of urbanization (i.e., when cities are small, and distance from city center to habitats of interest is short) both avian and hymenopteran communities increase in species richness ([Jokimaki and Suhonen, 1993;](#page-14-0) [Christie and](#page-12-0) [Hochuli, 2009\)](#page-12-0), potentially due to species-specific preferences for edge habitat [\(Sisk and Battin, 2002\)](#page-16-0). However, this increase is temporary and as urbanization continues communities typically decline in species richness ([Jokimaki and Suhonen, 1993\)](#page-14-0), although long-term changes to urban edge effects are understudied. Thus, current evidence suggests that species richness patterns may follow the intermediate disturbance hypothesis, while diversity patterns are most closely associated with the ecosystem-stress gradient hypothesis. Given these conflicting results, it is unclear how community resilience changes with urbanization. Further investigations that incorporate city-specific effects (e.g., human population dynamics, greenspace abundance and arrangement, city age) ([Leveau et al., 2017](#page-14-0)), seasonal and latitudinal changes in richness and diversity [\(Clergeau et al., 1998](#page-12-0); [Leveau and Leveau,](#page-14-0) [2016;](#page-14-0) [Leveau et al., 2017\)](#page-14-0), along with functional diversity indices and adaptive capacity metrics would be of great benefit to understanding the resilience dynamics of urban avian communities and may increase the accuracy of these hypotheses in predictive models.

2.1.2 Biotic Homogenization and Niche Filtering

Under either disturbance hypothesis, high levels of urbanization result in community disassembly through biotic homogenization (i.e., the process by which species within a given habitat become genetically, taxonomically, and functionally similar over time) [\(Olden et al., 2004](#page-15-0); [McKinney, 2006](#page-14-0)) and loss of species richness and functional diversity ([Figure 2](#page-5-0)) ([McKinney, 2002;](#page-14-0) [MicKinney, 2006;](#page-14-0) Ortega-Á [lvarez and MacGregor-Fors, 2009;](#page-15-0) [Sol et al., 2014\)](#page-16-0) which can fundamentally change the resilience and composition of communities across seasonal and long-term scales ([Olden et al., 2004](#page-15-0); [Leveau et al., 2021](#page-14-0)). Biotic homogenization is often linked to niche-filtering, the process by which abiotic factors act as a filter on biotic organisms, allowing only certain traits to persist and resulting in coexisting species being more similar than would be expected by chance ([Figure 2](#page-5-0)) ([Mouchet et al., 2010\)](#page-15-0). Many studies have highlighted the role of niche-filtering on urban avian communities ([McKinney, 2006\)](#page-14-0), with strong, homogenizing selection on foraging and nesting life history traits. In general, foraging strategies including granivory, omnivory, aerial insectivory, and ground-foraging are favored by urban habitats [\(Emlen, 1974](#page-13-0); Allen and O'[Connor, 2000](#page-12-0); [Chace and Walsh,](#page-12-0) [2006](#page-12-0); [Croci et al., 2008](#page-13-0); Guetté [et al., 2017\)](#page-13-0), while surfaceforaging insectivory and carnivory are selected against ([Lim](#page-14-0) [and Sodhi, 2004](#page-14-0); [Croci et al., 2008](#page-13-0)). Regarding nesting behaviors, both cavity-nesting and ground-nesting species are selected against in urban habitats [\(Tomasevic and Marzluff,](#page-16-0) [2017](#page-16-0)), due to the lack of available nest excavation sites (e.g., snags, [Tomasevic and Marzluff, 2017\)](#page-16-0) and appropriate, undisturbed ground-nesting habitat [\(Blewett and Marzluff,](#page-12-0) [2005](#page-12-0); [Evans et al., 2011\)](#page-13-0). However, secondary cavity nesting species such as the European starling (Sturnus vulgaris) and black-capped chickadee (Poecile atricapillus) may be more resistant to extirpation in urban habitats than primary cavity nesting species due to their use of anthropogenic cavities (i.e., nest boxes, cavities in human-built structures) ([Tomasevic and](#page-16-0) [Marzluff, 2017\)](#page-16-0). Furthermore, habitat specialists across taxa tend to be extirpated or have reduced abundances throughout urban environments ([Donnelly and Marzluff, 2006](#page-13-0); [Devictor et al.,](#page-13-0) [2007](#page-13-0)), likely due to habitat loss and resource limitations in homogenous urban habitats [\(Schneiberg et al., 2020\)](#page-15-0).

2.2 Avian Community Resilience in Response to and Following Urban Conversion

Traditional resilience metrics (i.e., resistance and recovery as typically applied to acute disturbances) are infrequently applied to urban conversion because the disturbance induced by urbanization is relatively permanent, making it difficult or impossible to measure community recovery ([Marzluff and](#page-14-0) [Ewing, 2008\)](#page-14-0). In heavily altered systems such as urban environments, measuring resilience of avian communities is complicated by the multifaceted biophysical (i.e., climate, species-interactions, physical processes, etc.) and socioeconomic (i.e., economic development, human

monk parakeet in the United States). Transitional stages of avian community composition are represented by (B, C), which demonstrate species loss and replacement, respectively, through the process of niche filtering (Created with [BioRender.com\)](https://BioRender.com).

demography, policies and regulation, etc.) influences on systems ([Alberti and Marzluff, 2004](#page-12-0)).

Resilience dynamics under urbanization change as the habitat is converted from natural to suburban to urban ([Figure 3](#page-6-0)). First, a primary disturbance occurs when urban conversion begins. Initial urban conversion is highly disruptive and natural communities have little ability to resist or recover from such extensive habitat destruction, resulting in significant permanent destructuring effects on communities ([McKinney, 2006\)](#page-14-0) and converting natural communities to alternative stable suburban communities. Subsequent continued urbanization events can then convert the suburban community to a stable urban community ([Figure 3](#page-6-0)). Suburban avian communities may have greater resistance to continued urban conversion because niche filtering has already begun, but this has not been explicitly investigated to our knowledge. Once urbanization is complete, communities typically reassemble to an alternative stable state (i.e., a novel community) that differs in composition and function from the original state (**Figures 2, [4](#page-6-0)**) (e.g., a stable urban system replacing a stable grassl[and](#page-13-0) system; Côté and [Darling, 2010;](#page-13-0) [Lugo et al., 2012](#page-14-0)), with little, if any opportunity to recover to the original state. Changes in species assemblages have been noted by [Lugo et al. \(2012\)](#page-14-0) in Puerto Rican ecosystems, where communities of plants, birds, and reptiles shift to novel assemblages following extensive land-use change for urban or agricultural development. Following this reassembly, urban avian communities may differ in their

resilience capacity and subsequent response to future disturbances [\(Alberti and Marzluff, 2004\)](#page-12-0). As urbanization and the strength of niche filtering increases, avian communities become less diverse in regard to life-history characteristics [\(Clergeau et al., 2006](#page-12-0); Ortega-Á [lvarez and MacGregor-Fors,](#page-15-0) [2009](#page-15-0); [Sol et al., 2014](#page-16-0)), resulting in a loss of functional groups and correlated community resilience (Figure 2) [\(Allen et al.,](#page-12-0) [2005](#page-12-0)). These effects can be compounded by interactions between urbanization and other anthropogenic factors, such as environmental toxins ([Møller, 2019\)](#page-14-0). Consequently, the resilience of avian communities to subsequent disturbance is predicted to decrease as urbanization increases.

Species-specific vulnerability to urban conversion also probably plays a role in determining community resilience in urban conversion but is relatively untested in urban resilience assessments. In birds and bats, vulnerability and adaptability to urban habitats are likely trait-mediated ([Jung and Kalko, 2011;](#page-14-0) [Jung and Threlfall, 2018](#page-14-0); [Paton et al., 2019;](#page-15-0) [Tai et al., 2022](#page-16-0)), but interplay between reproductive, migratory, physiological, and foraging traits determine risk of extirpation from urban habitats [\(Brown and Graham, 2015\)](#page-12-0). Trait-vulnerability relationships vary among geographic regions (Gonzá[lez-Oreja, 2011](#page-13-0)), and mechanisms underlying these relationships are unknown. More specifically, experimental studies are necessary across species and geographic areas before generalizations regarding trait-mediated vulnerabilities to urban conversion can be formed [\(Seress and](#page-16-0) [Liker, 2015;](#page-16-0) [Rega-Brodsky et al., 2022\)](#page-15-0).

FIGURE 3 | Conceptual diagram of resilience in urban habitats, illustrated by a ball-cup analogy and loosely modeled after [Figure 1](#page-2-0) of [Gunderson \(2000\)](#page-13-0). Communities in undeveloped habitats have little resistance to urban conversion and are quickly converted to suburban, then urban communities (although the suburban state can be skipped). Urban communities then require significant energy input to transition to another community state (e.g., through habitat restoration, shown by the steep rightward slope) or to recover to the original, pre-urbanization community (i.e., the steep leftward slope). In most instances recovery to the original community is not observed because urban habitats are rarely reverted to natural, undeveloped states. The steepness of these slopes may decrease with the use of green infrastructure and other habitat improvements, allowing an urban community to transition to a suburban state or a new, semi-urban state.

2.3 Complexities in Predicting the Effects of Urban Conversion on Avian Communities and Resilience

There are numerous complexities in urban conversion that make predicting community-level resilience and outcomes difficult. Many of these topics are understudied or discussed inconsistently in the

existing avian literature, s and we echo the calls of other researchers (i.e., [Rega-Brodsky et al., 2022](#page-15-0)) to encourage future research in these areas. Better accounting for these complexities in future studies will be essential for thoroughly understanding the resilience dynamics of avian communities in urban systems, and we suggest the following areas for future study:

following a loss of diversity would exhibit high recovery (Created with BioRender.com).

all community members may persist, unchanged; these communities would exhibit high resistance. Communities that exhibit later reassembly or persistence

1. Incorporation of the concept of recovery into studies of urbanization. This can be difficult, because effects are heterogeneous and the conversion to urban habitats is relatively permanent. However, the restoration of community function following urbanization is relatively unexplored.

2. Multi-scale studies ([Hostetler and Holling, 2000](#page-13-0); [Melles](#page-14-0) [et al., 2003](#page-14-0)) that incorporate temporal (e.g., time of sampling, age of urban habitats), socioeconomic and land-use factors [\(Kang](#page-14-0) [et al., 2015;](#page-14-0) [Schütz and Schulze, 2015\)](#page-15-0) into ecological studies of urbanization ([Leveau, 2018](#page-14-0)).

3. Investigations into the multi-trophic effects on communities of exotic/invasive expansion in urban habitats, and their implications for community resilience. Human mediated dispersal of exotic species can strongly affect avian community structure in urban habitats [\(Donnelly and Marzluff,](#page-13-0) [2006;](#page-13-0) [Schneiberg et al., 2020](#page-15-0)). Dominance of exotic plants and birds in urban habitats is well-documented ([Green and Baker,](#page-13-0) [2003](#page-13-0); [Banerjee and Dewanji, 2017\)](#page-12-0) and these species can negatively impact native avifauna, through resource competition, predation, or other disturbance ([Yap and Sodhi,](#page-16-0) [2004\)](#page-16-0). Invasive species also disrupt avian community reassembly through limitations on prey species (e.g., invasive plants often outcompete native plants, leading to population declines in both invertebrates and their avian predators ([Litt et al., 2014;](#page-14-0) [Møller,](#page-14-0) [2019\)](#page-14-0), nesting habitat, or foraging habitat [\(Litt et al., 2014](#page-14-0); [Schneider and Miller, 2014](#page-15-0)). Although some invasive plants may provide refugia for forest species or understory-nesting birds in urban habitats, these effects are species-specific and vary seasonally ([McCusker et al., 2010](#page-14-0)).

4. Increased studies occurring in the global south and non-English speaking countries. There is extensive geographic bias in the existing urban ecology literature ([Rega-Brodsky et al., 2022\)](#page-15-0), with studies occurring in the global north (Nearctic and Paleartic), and English speaking countries being overrepresented, despite many biodiversity hotspots and larger human populations being located in tropical, southern regions [\(Rega-Brodsky et al., 2022](#page-15-0)).

3 CLIMATE CHANGE AND AVIAN COMMUNITY RESILIENCE

The current climate is warming at a rate unprecedented in the last 2000 years [\(Masson-Delmotte et al., 2021](#page-14-0)), producing a plethora of climatic changes, including an increase in average precipitation over land, more frequent and intense precipitation events, more frequent concurrent heatwaves and droughts, sea level rise, shifts in storm tracks, and poleward shifts in climate zones [\(Masson-Delmotte et al., 2021\)](#page-14-0). Over the next century climatic changes are expected to continue and intensify as temperatures increase 1.0 - 5.7°C by 2100 ([Masson-Delmotte](#page-14-0) [et al., 2021](#page-14-0)), resulting in the disappearance of some present climates and the creation of "novel" climates not currently experienced ([Williams et al., 2007](#page-16-0)). Many studies have investigated species-specific responses to climatic changes due to global warming, the results of which are already reviewed by numerous others (e.g., [Crick, 2004](#page-13-0); [Jiguet et al., 2006;](#page-14-0) [Leech and](#page-14-0)

[Crick, 2007;](#page-14-0) [Reif, 2013;](#page-15-0) [Scridel et al., 2018;](#page-15-0) [Maxwell et al., 2019\)](#page-14-0). Here, we provide a brief overview of vulnerability and resilience at the species level, then discuss these within the context of avian community impacts and resilience.

3.1 Vulnerability of Bird Species to Climate Change: Exposure and Sensitivity

Vulnerability assessments are a key method for evaluating extinction risk under climate change scenarios and prioritizing conservation actions [\(Foden et al., 2019](#page-13-0)). Various definitions of vulnerability exist ([Williams et al., 2007](#page-16-0)), but the Intergovernmental Panel on Climate Change (IPCC) defines vulnerability as "the predisposition to be adversely affected" [\(Oppenheimer et al., 2014](#page-15-0)). The vulnerability of species to climate change is typically viewed as a combination of exposure to changing climatic means and extremes (e.g., geographic distribution of the species, climatic niche) and the intrinsic sensitivity of the species (e.g., physiological limits, life history, specialization, and obligate species interactions) [\(Reif, 2013\)](#page-15-0).

3.1.1 Exposure of Avian Species to Changing Climatic Means and Extremes

Regarding exposure, birds inhabiting poleward portions of continents and tropical montane regions are projected to experience disappearing climates over the next century ([Williams et al., 2007\)](#page-16-0), and are at high risk of extinction associated with climate change [\(Sekercioglu et al., 2012;](#page-16-0) [Reif,](#page-15-0) [2013;](#page-15-0) [Freeman et al., 2018\)](#page-13-0). Tropical montane species are expected to be vulnerable to the effects of climate change due to the historic stability of temperatures, smaller range sizes near the equator [\(Williams et al., 2007\)](#page-16-0), and limited extents of occurrence at high elevations [\(Sekercioglu et al., 2008\)](#page-16-0), which create more narrow endemism in climatic and geographic space [\(Willams et al., 2007\)](#page-16-0). While exposure is typically estimated broadly for all species within a geographic area, microhabitat and physiological buffering strategies can also influence exposure ([Riddell et al., 2021\)](#page-15-0). For example, small mammals are predicted to be less vulnerable to warming and drying due to climate change than sympatric birds because of their lower thermoregulatory cooling costs and the buffering effects of underground burrowing ([Riddell et al., 2021](#page-15-0)).

3.1.2 Sensitivity of Avian Species to Changing Climatic Means and Extremes

Regarding sensitivity, species with broad thermal tolerance and higher thermal maximums appear to be less sensitive to dramatic changes in temperature and steady increases in average temperature than those with narrow thermal tolerance and lower thermal maximums [\(Jiguet et al., 2006;](#page-14-0) [Jiguet et al.,](#page-14-0) [2007](#page-14-0)). For example, during an extreme heatwave in France, bird species with small thermal ranges exhibited the sharpest decreases in population growth rate in correspondence with highest temperatures ([Jiguet et al., 2006\)](#page-14-0). Of course, climate change effects are not limited to changes in temperature, but also include increases in extreme weather events with most studies

reporting negative effects on bird populations ([Maxwell et al.,](#page-14-0) [2019\)](#page-14-0). Sensitivity of bird species and guilds to extreme weather will depend on timing and type of event (e.g., drought, flooding, cyclone, fire) and species-specific characteristics (e.g., habitat, foraging guild, life history traits).

Life history traits are also critical components of sensitivity to the impacts of climate change ([Foden et al., 2013;](#page-13-0) Pacifi[ci et al.,](#page-15-0) [2015](#page-15-0)). Many bird species that are habitat specialists, have fast life histories, or are single brooded are currently in decline and climate change impacts can explain a significant portion of these declines ([Reif, 2013\)](#page-15-0), but habitat type and migration strategy have little impact on projected future responses to climate change [\(Langham](#page-14-0) [et al., 2015\)](#page-14-0). Habitat specialists are limited in their ability to adjust to climatic changes by immigrating to new habitats or exploiting novel resource bases, and competition induced by differential responses to these changes may favor generalist species [\(Warren](#page-16-0) [et al., 2001](#page-16-0); [Clavel et al., 2011\)](#page-12-0). Regarding life history speed, population growth rates of birds with fast life histories are more sensitive to climate-induced changes to demographic rates, such as growth, survival, and reproduction [\(Morris et al., 2008](#page-15-0); [Sekercioglu et al., 2012](#page-16-0)), and their shorter lifespans allow for fewer opportunities to learn and adjust to directional environmental changes [\(Jiguet et al., 2007\)](#page-14-0), such as shifts in peak food availability ([Visser et al., 2004\)](#page-16-0). For example, blue tits can learn the best breeding date through experience of mistiming ([Grieco et al., 2002](#page-13-0)); but for short-lived birds such as these, most breeders are young without previous experience to learn from ([Visser et al., 2004](#page-16-0)). However, species with fast life histories are also frequently multi-brooded with larger clutches, traits that increase their adaptive capacity and thus, the probability of recovery from mortality associated with extreme weather events and other climate change effects [\(Angert et al., 2011;](#page-12-0) [Sekercioglu](#page-16-0) [et al., 2012](#page-16-0)). Thus, although species with fast life histories may be more sensitive to climate change impacts they may also recover more quickly.

3.2 Responses of Avian Species to Climate Change: Adaptive Capacity and Extinction

The combination of exposure and sensitivity to climate change is highly species-specific, and thus, species' responses to climate change are predicted to be idiosyncratic [\(Williams et al., 2007\)](#page-16-0). Faced with novel climatic conditions, a species can respond with tolerance in situ through behavioral and physiological adaptation or plasticity, shifts in phenology, habitat, and/or geographic distributions, and/or extinction if these mechanisms fail [\(Jackson](#page-13-0) [and Overpeck, 2000](#page-13-0); [Moritz and Agudo, 2013\)](#page-15-0). Tolerance depends in large part on the adaptive capacity of the species [\(Gallopin, 2006](#page-13-0); [Carpenter and Brock, 2008](#page-12-0); [Thurman et al., 2020\)](#page-16-0), which is primarily determined by the propensity of a species for genetic adaptation, phenotypic plasticity, and dispersal ([Beever et al., 2016\)](#page-12-0).

3.2.1 Genetic Adaptation in Response to Climate Change

Genetic adaptation is predicted to be a critical determinant of species' resilience to climate change ([Vedder et al., 2013](#page-16-0); [Merila](#page-15-0) [and Hendry, 2014;](#page-15-0) [Meester et al., 2018\)](#page-14-0). Direct evidence of genetic adaptation to climate change is scarce [\(Charmantier](#page-12-0) [and Gienapp, 2014](#page-12-0); [Merila and Hendry, 2014\)](#page-15-0), but has been observed in at least one wild bird species, the tawny owl, Strix aluco [\(Karell et al., 2011](#page-14-0)). The capacity to genetically track climate change is expected to depend on the species' generation time, population size, genetic variation, and genetic correlations between traits [\(Meester et al., 2018](#page-14-0)). All else being equal, smaller birds with relatively short generation times, large populations, and large pools of genetic variation will have a higher capacity for rapid genetic response to climate change than those with long generation times and/or small populations [\(Vedder et al., 2013](#page-16-0); [Meester et al., 2018](#page-14-0)). Although adaptation to climate change effects may rescue some vulnerable species from extinction, adaptation also has costs at both the population and individual levels. For example, selection can reduce population sizes and genetic variation, decreasing capacity for response to future stressors and increasing risk of species extinction. Evolutionary trait change can also have costs associated with tradeoffs, pleiotropy, or linkage. Thus, while genetic adaptation may provide a buffer against climate change and is a critical component of adaptive capacity, it will not guarantee survival [\(Meester et al., 2018](#page-14-0)) and may contribute only weakly to rapid responses in multicellular organisms ([Merila and](#page-15-0) [Hendry, 2014](#page-15-0)).

3.2.2 Phenotypic Plasticity in Response to Climate Change

Rapid responses may be more strongly affected by phenotypic plasticity, which can occur over a shorter time period than genetic adaptation and is also predicted to be a critical determinant of species' resilience to climate change ([Vedder](#page-16-0) [et al., 2013;](#page-16-0) [Merila and Hendry, 2014;](#page-15-0) [Meester et al., 2018\)](#page-14-0). Selection can increase or decrease phenotypic plasticity through genetic change. Thus, phenotypic plasticity and genetic adaptation are intrinsically related, but often operate on different temporal scales ([Meester et al., 2018](#page-14-0)), with phenotypic plasticity being the more rapid of the two. Phenotypic plasticity may be sufficient for some birds to persist in situ in the face of climate change ([Vedder et al., 2013\)](#page-16-0), although not sufficient for all organisms (e.g., trees, [Duputie](#page-13-0)́ [et al., 2015;](#page-13-0) ectotherms, [Gunderson and Stillman, 2015](#page-13-0)). However, plastic responses will only remain adaptive if environmental cues remain reliable and informative. Climate change may disrupt the detection of cues, or their reliability through a variety of mechanisms. If cue reliability decreases, selection can drive accompanying decreases in plasticity, or mismatches with the optimum phenotype in a fluctuating environment could lead to population extinction [\(Bonamour](#page-12-0) [et al., 2019\)](#page-12-0). Evolution of adaptive phenotypically plastic shifts in optimal reproductive timing have been reported in at least one wild bird (the great tit, *Parus major*) [\(Nussey et al., 2005;](#page-15-0) [Charmantier et al., 2008\)](#page-12-0). Overwhelmingly, however, direct evidence of both phenotypic plasticity and microevolution in avian responses to the effects of climate change are lacking, despite widespread discussion of their importance [\(Charmantier](#page-12-0) [and Gienapp, 2014\)](#page-12-0).

3.2.3 Dispersal in Response to Climate Change

Dispersal propensity also influences the adaptive capacity of a species to a changing climate, by affecting its ability to track shifting climate envelopes ([Leech and Crick, 2007;](#page-14-0) [Beever et al.,](#page-12-0) [2016\)](#page-12-0). Current climate change is already producing observable systemic shifts in plant and animal phenology [\(Root et al., 2003](#page-15-0); [Crick, 2004;](#page-13-0) [Root et al., 2005](#page-15-0); [Leech and Crick, 2007](#page-14-0)) and species distributions (e.g., [Parmesan and Yohe, 2003](#page-15-0); [Hickling et al., 2006](#page-13-0); [Leech and Crick, 2007;](#page-14-0) [Freeman et al., 2018](#page-13-0)), with range shifts averaging 6.1km per decade toward the poles for birds, butterflies, and alpine herbs ([Parmesan and Yohe, 2003\)](#page-15-0). At least some bird species are shifting their distributions and community compositions to track moving climate envelopes, although not quickly enough to match the rate of climate change [\(Devictor et al., 2008;](#page-13-0) [Santangeli](#page-15-0) [and Lehikoinen, 2017](#page-15-0)). Dispersal ability in response to climate change appears to be highly idiosyncratic across bird species, depending on region, climatic constraints, and species-specific traits ([Brotons et al., 2019](#page-12-0)). Migratory species may have greater dispersal potential, because of their greater mobility ([Sekercioglu](#page-16-0) [et al., 2008](#page-16-0)), and indeed, migratory bird species are currently at a lower risk of extinction than sedentary species ([Sekercioglu, 2007\)](#page-15-0). However, migratory species may also be restricted in their capacity for phenological shifts in response to climate change ([Leech and](#page-14-0) [Crick, 2007](#page-14-0)). Because climatic changes are not spatially or temporally monotonic [\(Burkett et al., 2005\)](#page-12-0), mismatches between the relative timing of cues for spring migration and periods of peak food availability on the breeding grounds may occur.

3.3 Methods to Predict Impacts of Climate Change on Avian Communities

Two approaches are predominantly used to predict the impacts of climate change on bird communities. The first utilizes singlespecies studies and extrapolates to communities, assuming that the response of single species can be applied across all species ([Jenouvrier, 2013](#page-13-0)). Secondly, modeling methods can be used to predict impacts for entire communities (e.g., joint species distribution models) ([Brotons et al., 2019\)](#page-12-0). Various modeling techniques have been used to predict changes in community structure and function under future climate change scenarios, including space-for-time substitution and the community temperature index (CTI) approach. CTI reflects the dominance of warm- and cold-dwelling species in a community and has been used to investigate changes in community structure in relation to shifting climate [\(Devictor et al., 2008](#page-13-0); [Santangeli and](#page-15-0) [Lehikoinen, 2017](#page-15-0)).

3.4 Impacts of Climate Change on Avian Communities

Climate constrains the fundamental niche of each species, and multivariate changes in climate are expected to result in community disassembly and reassembly because of speciesspecific shifts in distribution, abundance, and extinction ([Figure 4](#page-6-0)) ([Root et al., 2003](#page-15-0); [Williams et al., 2007](#page-16-0)). This conceptual framework is supported by evidence from the last deglaciation in which climates with no modern analogs produced plant associations and vegetation biomes with no modern

analogs [\(Overpeck et al., 1992](#page-15-0); [Williams et al., 2001;](#page-16-0) [Bush](#page-12-0) [et al., 2004\)](#page-12-0). Given that temperature is currently increasing at a rate greater than that of the last 2000 years ([Masson-Delmotte](#page-14-0) [et al., 2021](#page-14-0)), species extinction rates and community reorganization are predicted to increase accordingly [\(Pimm,](#page-15-0) [2009](#page-15-0)). Here, we examine the predicted and observed impacts of climate change on avian species richness, turnover (i.e., community reassembly), and function.

Many studies have examined the projected change in number of species (e.g., extinction rate) and changes to species' geographic distributions under different climate scenarios, which can be used to estimate changes in species richness (e.g., [Stralberg et al., 2015;](#page-16-0) [Massimino et al., 2017](#page-14-0)). Most predict an increase in the proportion of high-temperature dwelling species [\(Devictor et al., 2008](#page-13-0); [Bowler et al., 2018\)](#page-12-0), a reduction in species ranges, and a decrease in species richness ([Brotons et al., 2019\)](#page-12-0). However, the ability of birds to disperse to new suitable habitat is a crucial factor of these models, and assumptions of no dispersal or total dispersal can completely reverse the outcome regarding species richness ([Barbet-Massin et al., 2009](#page-12-0); [Brotons et al., 2019\)](#page-12-0). For vegetation specialists, immigration will be limited by the often much slower dispersal rates of associated vegetation ([Root](#page-15-0) [and Schneider, 2002\)](#page-15-0). In contrast, vegetation generalists will have much greater dispersal ability. Where avian communities include both vegetation-specialists and generalists, immigration rate ([Root and Schneider, 2002](#page-15-0)) and changes in abundances ([Bowler et al., 2018\)](#page-12-0) will differ greatly among community members and the potential for community turnover (i.e., disassembly and reassembly) is high ([Figure 4](#page-6-0)) ([Root and](#page-15-0) [Schneider, 2002](#page-15-0)). Still other species may persist in place through phenotypic plasticity or genetic adaptation ([Brotons](#page-12-0) [et al., 2019](#page-12-0)), and where communities are composed of species with varying degrees of phenotypic plasticity and capacity for genetic adaptation, species turnover may also be high ([Figure 4](#page-6-0)). Such independent shifts in species distributions are predicted to result in the rapid development of novel species assemblages, with potentially dramatic consequences for species interactions and ecosystem function ([Brotons et al., 2019](#page-12-0)).

Bird assemblages fulfill critical sets of ecological functions for ecosystems, which can be altered following community disassembly and/or reassembly ([Barbet-Massin and Jetz, 2015;](#page-12-0) [Brotons et al., 2019\)](#page-12-0). Under the IPCC's Fourth Assessment Report emission scenario A2 [\(IPCC, 2007](#page-13-0)), avian assemblage functional structure is projected to change highly unevenly across space, sometimes resulting in substantial loss of functional diversity ([Barbet-Massin and Jetz, 2015\)](#page-12-0). Tropical and subtropical biomes are predicted to be especially hard hit by losses in functional diversity, while range expansions may compensate in high latitude regions [\(Barbet-Massin and Jetz,](#page-12-0) [2015\)](#page-12-0). Dietary guilds are also projected to change heterogeneously under continued current greenhouse gas emissions, with decreases predominantly in primary and mixed consumer guilds, and increases in high-level consumers ([Ko](#page-14-0) [et al., 2014](#page-14-0)), although these projections are dependent on geographic region and assumptions regarding dispersal distance [\(Ko et al., 2014\)](#page-14-0).

3.5 Resilience of Avian Communities to Climate Change: Resistance and Recovery

Most studies on the resilience of avian communities to climate change have focused on resistance over recovery, because (1) the window between extreme climatic events may become so short that recovery is unlikely, and (2) many climate disturbances will not be acute, providing little role for recovery (Côté [and Darling, 2010\)](#page-13-0). The resistance of avian communities will depend on the interactive effects of species vulnerability (i.e., sensitivity and exposure) and adaptive capacity (e.g., plasticity, genetic diversity, dispersal abilities), the ability of the vegetative community to shift phenology/geography in concert with the avian community, and the ability of the community to compensate for lost species and open niches (e.g., functional evenness, diversity, and redundancy) ([Figure 4](#page-6-0)). The probability of community disassembly will naturally be higher where species' vulnerability to climate change is also high, such as in poleward and tropical montane regions [\(Williams et al., 2007\)](#page-16-0), thus species exposure and sensitivity are critical to determining community resiliency. Novel communities are predicted to develop in response to novel climates [\(Hobbs et al.,](#page-13-0) [2006\)](#page-13-0), which are projected to be concentrated in the tropics and subtropics ([Williams et al., 2007](#page-16-0)). For species with high vulnerability, resistance to climate change may be low, but adaptive capacity and human intervention can provide a road to recovery. Appropriate adaptive and plastic responses may occur over a longer time scale than climate change [\(Jackson and](#page-13-0) [Overpeck, 2000;](#page-13-0) [Williams et al., 2007\)](#page-16-0), leading to temporary community disassembly and decreases in species' population sizes, followed by recovery once appropriate responses occur.

3.6 Complexities in Predicting Avian Community Resilience to Climate Change

A number of issues are in need of increased study to improve predictions of avian community response and resilience to climate change:

1. The majority of current research efforts on plant and animal responses to climate change focus on first order effects of global warming, especially temperature and precipitation changes. However, second and higher order effects also directly influence plant and animal community composition and function ([Burkett et al., 2005](#page-12-0)). For example, as the global temperature rises, so too does sea level, leading to increases in coastal sediment and water salinity and selection for species with higher salinity tolerance [\(Burkett et al., 2005](#page-12-0)).

2. Climate change is often non-linear ([Burkett et al., 2005\)](#page-12-0) and acts on bird communities via both direct effects and indirect ecological cascade effects ([Brotons et al., 2019\)](#page-12-0). Increased research is needed on these indirect effects of climate change.

3. Finally, responses of species and communities to climate change will depend on local biotic and abiotic factors, including chemical pollution ([Noyes and Lema, 2015\)](#page-15-0), disease and pest outbreaks [\(Harvell et al., 2009\)](#page-13-0), invasive species, land-use changes, and alterations in disturbance regimes [\(Brotons et al.,](#page-12-0) [2019\)](#page-12-0). Research on the interactions between these factors at local scales, and modeling and larger geographic scales is needed to accurately predict community response.

4 URBANIZATION AND CLIMATE CHANGE INTERACT TO AFFECT AVIAN COMMUNITY RESILIENCE

Many studies fail to consider the interactive effects of climate change and urban conversion ([Felton et al., 2009](#page-13-0)) and disentangling their relative impacts and importance can be difficult [\(Hockey et al., 2011;](#page-13-0) [Brotons et al., 2019](#page-12-0)). For many species, interactions between these two drivers of community change are expected to amplify the effects of each on temperature change and habitat loss, creating a deadly "anthropogenic cocktail" [\(Travis, 2003](#page-16-0)), although positive or balancing effects are also possible [\(Clavero et al., 2011](#page-12-0)).

4.1 Negative Interactive Effects of Urbanization and Climate Change: Temperature and Habitat Loss

Habitat loss, such as through urban conversion, can induce de facto climate change effects by driving relocation of species to less suitable habitats, causing subsequent niche restriction, increased susceptibility to climate change [\(White et al., 2014\)](#page-16-0), and altering species assemblages. Communities that are forced into or choose to move into urban environments typically experience higher temperatures than those in undeveloped habitats, which can exacerbate the warming effects of climate change [\(Leveau et al.,](#page-14-0) [2021](#page-14-0)), and induce species turnover/loss in the community. For example, urban and agricultural avian communities have proportionally more warm-adapted species than forest dwelling avian communities in the European Mediterranean ([Clavero](#page-12-0) [et al., 2011](#page-12-0)). We see this also in England, where avian communities have suffered a steep loss of cold-adapted species, in part due to thermal effects of both land-use change and climate change [\(Oliver et al., 2017\)](#page-15-0). Anthropogenic land use changes can also decrease resilience to climate change by fragmenting or destroying remaining habitat for communities that are predicted to experience diminishing ranges under climate change ([Jetz et al., 2007](#page-14-0)), and restricting the ability of communities to track moving climate envelopes [\(Roberts et al.,](#page-15-0) [2019](#page-15-0)). These effects will be most evident for habitat specialist communities that are limited by vegetation dispersal. Coastal prairie communities in North America, for example, rely on unique sandy soils and appear to be restricted in shifting northward because of coastal landscape fragmentation and urban conversion ([Roberts et al., 2019](#page-15-0)). Similarly, saltmarsh specialists could theoretically exhibit high resilience to rising sea levels by moving inland, but are often limited by anthropogenic coastal development, leading to saltmarsh reduction and simultaneous reduction of saltmarsh specialist communities ([Thorne et al., 2012](#page-16-0); [Rosencranz et al., 2018](#page-15-0)).

4.2 Positive and Balancing Interactive Effects of Urbanization and Climate Change

Although the interactive effects of climate change and human induced disturbance such as urbanization are widely considered to have strongly negative effects for most avian communities,

positive effects are possible. For example, evidence in coral reef communities suggests that anthropogenic disturbance can increase resilience to climate change by selecting for the most resilient phenotypes (Côté [and Darling, 2010\)](#page-13-0). Additionally, urban habitats may provide relatively stable refugia for urban exploiters to replace or subsidize habitat made unsuitable by climate change. Purple martins (Progne subis), for example, are increasing their use of urban areas for nesting and migratory staging ([Bridge et al., 2016](#page-12-0)) and displaying phenotypically plastic migration timing in association with rising global temperatures ([Fraser et al., 2019](#page-13-0)). The simultaneous effects of land use change and climate change can also be balancing; for example, in Danish avian communities, agricultural land use change decreases species abundances, while warmer winters increase species abundances [\(Bowler et al., 2018\)](#page-12-0). Thus, land use changes can increase, decrease, or maintain the resilience of avian communities in the face of climate change [\(Clavero et al.,](#page-12-0) [2011\)](#page-12-0) in species-specific ([Yalcin and Leroux, 2018](#page-16-0)) and habitat-specific manners ([Kampichler et al., 2012\)](#page-14-0).

5 DISCUSSION

Ecological resilience has the potential to be a useful metric for assessing the current and predicted future state of an ecological community in response to disturbances, such as urbanization and climate change. Resilience has direct, oftentimes complex, interactions with other concepts such as adaptive capacity, the ecosystem stress-gradient hypothesis, and the intermediate disturbance hypothesis, which are in need of increased examination. In this review, we focus on avian communities because birds are sensitive to environmental change ([Foden et al.,](#page-13-0) [2013](#page-13-0)) and resilience studies at the scale of the ecological community are generally lacking ([Allen et al., 2005;](#page-12-0) [Fischer](#page-13-0) [et al., 2007\)](#page-13-0). Existing research suggests strong heterogeneity in the responses and resilience of bird communities to urban conversion and climate change, depending on a variety of species-specific and community-level mechanisms that interact to determine outcomes ([Figure 1](#page-2-0)). Moving forward, we see three primary issues hindering forward momentum in this field: (1) implementation of standardized methods of quantifying resilience, (2) unknowns surrounding responses of communities to chronic disturbance across ecological (e.g., species to communities) and geographic (e.g., local to regional) scales, and (3) unknowns surrounding interactions between community resilience and socio-ecological factors. Considering these factors, we recommend five directions for future studies:

(1) Incorporation of both adaptive capacity and measures of functional diversity in definitions of community resilience. The development of a more comprehensive community resilience index would allow for synchronization across studies that would facilitate replication and meta-analyses.

(2) Measurement and/or modeling of both resistance and recovery in urbanization and climate change studies that focus on ecological communities. Recovery is especially understudied, specifically whether avian communities can reassemble and

resume original ecosystem functions, and factors that facilitate recovery. This will most likely be accomplished through longterm ecological studies of communities.

(3) Multiscale and/or multitaxa studies including three-way interactions between plants, animals, and climate are needed. For example, coastal vegetation community structure is shifting in response to sea level rise and changes in salinity [\(Burkett et al.,](#page-12-0) [2005](#page-12-0)), but we have little understanding of how coastal marsh bird communities are responding to climate change-associated drivers ([Woodrey et al., 2012](#page-16-0)), or how these responses interact with changes in vegetation and competitive dynamics. Resilience measurements (incorporating both adaptive capacity and functional diversity) for both plant and animal species in a defined spatial extent alongside relevant climate and/or landuse variables may provide a more thorough understanding of the effects and interplay of these factors.

(4) Additional evaluations and predictions of ecological resilience that incorporate interactions between anthropogenic changes (e.g., climate change, urbanization, pollution). Section 4 of this review provides several examples of such studies.

(5) Increased understanding of the interactions between ecological resilience and measurable socio-ecological dynamics (e.g., regional socioeconomics, ecotourism, and human use of greenspace, see [Ostrum, 2009](#page-15-0) and [McGinnis and Ostrom, 2014](#page-14-0) for an extensive list of factors and socio-ecological system framework explanations) [\(Cote and Nightingale, 2012](#page-13-0)). For example, regional socio-economics can interact with species life histories to affect abundances in birds ([Chaudhary and](#page-12-0) [Gutzwiller, 2020\)](#page-12-0). Research like this could be ecologically scaled up to the community level to make broader predictions of community resilience and recovery to anthropogenic change and socio-ecological dynamics, and/or geographically scaled down to provide specific predictions for local communities.

AUTHOR CONTRIBUTIONS

MM spearheaded the development of the concepts presented in this review. MM, JG, and RA all contributed to literature review and manuscript preparation, with MM responsible for Section I (introduction), RA responsible for Section II (urbanization), JG responsible for Section III (climate change), RA and JG responsible for Section IV (urbanization and climate change interactions), and MM responsible for Section V (discussion). MM, RA, and JG all contributed equally to the editing process and to the development of figures and tables. MM acted as corresponding author and was responsible for the submission process. All authors contributed to the article and approved the submitted version.

FUNDING

Funding for this review was made possible by MM's graduate research fellowship through the Rob & Bessie Welder Wildlife Foundation.

ACKNOWLEDGMENTS

We would like to thank the Rob and Bessie Welder Wildlife Foundation for fellowship support to MM, and the Texas A&M Office of Graduate Studies for fellowship support to RA. This

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manuscript is Rob and Bessie Welder Wildlife Foundation Contribution number 729. We would also like to thank Dr. Mary Ann Ottinger, Dr. J. Kenneth Grace, and members of the Grace Lab for their feedback on this manuscript, and the anonymous reviewers for their constructive comments and suggestions.

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