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Biomass and abundance trends diverge as the North American avifauna undergoes widespread demographic declines

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Biomass is a fundamental metric in ecology and conservation, widely used to inform questions related to community structure, energetics and function. Despite the ubiquity of biomass in broader ecological research, avian ecology and conservation has been based primarily on measures of abundance. Here, we re-examine a recent study in avian conservation that found a net loss of three billion North American birds from 1970–2017. We augment this analysis by calculating change in overall avian biomass during the same period. Counterintuitively, we find that avian biomass across the continent has increased by 11% despite a 29% decline in abundance. Substantial restructuring in the biomass of trophic communities has occurred, with herbivores, omnivores, vertivores, frugivores and scavengers seeing net increases, while invertivores, granivores, nectarivores and aquatic predators have exhibited declines. We suggest that avian biologists can benefit from increased inclusion of biomass as a metric of trophic- and community-level ecosystem function.

Keywords: biomass flux, biomass trends, community restructuring, ecosystem function, three billion birds

Introduction

Biomass – the collective weight of organisms in a given system – is often used as an indicator of ecosystem function and status across taxa and at varying spatial scales (Hicke et al. 2002). Measures of community-wide biomass are useful in a variety of contexts within conservation ecology, from evaluating the response of communities to management efforts (McClanahan and Graham 2015), to calculating change from historical baselines (Lotze and Worm 2009). The use of biomass in conservation is informed by the central role it plays in ecological theory, specifically for understanding food chain energetics, trophic cascades and biomass pyramids (Barbier and Loreau 2019, Galiana et al. 2021), and underpinning the metabolic theory of ecology (Brown et al. 2004). As such, biomass is widely studied across plants, marine invertebrates, insects, fish, and mammals (Hatton et al. 2015, Bar-On et al. 2018, Bianchi et al. 2021, Maschler et al. 2022, Greenspoon et al. 2023, Müller et al. 2024).

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However, despite robust early interest from ornithologists in the early- and mid-20th century (Emlen 1972, Willson 1974, Beissinger and Osborne 1982, Maurer and Brown 1988), the study of biomass in avian ecology is generally uncommon today, albeit with notable exceptions (Inger et al. 2015, Ng et al. 2022, Gregory et al. 2023).

Despite constituting a relatively small proportion of animal biomass globally (Bar-On et al. 2018), the biomass of birds is especially important in a variety of ecosystem services and functions, including energy transfer across trophic levels and spatial scales (Sekercioglu et al. 2016). Demographic changes among large species in particular can play an outsized role in structuring ecosystems by dramatically altering the total amount of energy, the rate of energy flow, and the spatial redistribution of energy in a system (Enquist et al. 2020). For example, migratory birds move extraordinary amounts of energy seasonally, which is more related to their total biomass rather than abundance (Ng et al. 2022). Measuring avian biomass across space and time provides an additional community structure and energy transfer that is missed by traditional abundance and biodiversity metrics and may be particularly useful in an era of rapid anthropogenic change (Hatton et al. 2015). At the extreme, changes in the relative distribution of biomass across trophic groups can be an early indicator of ecosystem collapse (Nagelkerken et al. 2020). Greater consideration of biomass in studies on global change could help widen the focus of avian conservation from the protection of individual species to more explicitly include the monitoring and preservation of ecosystems and their functioning.

Quantifying biomass can provide additional context to interpretations of abundance trends at any geographic or temporal scale, but perhaps especially as avian research increasingly scales up to study hundreds or thousands of species across continents (Morelli et al. 2021) in an era of global anthropogenic change. Measures of avian biomass are readily obtainable by simply multiplying published estimates of the body weight of species by estimates of abundance, which provides a measure of the total energy contained in a group of organisms, as well as the relative distribution of mass across trophic levels or other groupings. Direct comparisons of abundance and biomass trends may be particularly fruitful, as the two metrics are not always strongly positively correlated (Saint-Germain et al. 2007, Inger et al. 2015, Gregory et al. 2023). The causes, consequences, and implications of abundance declines may be interpreted very differently if biomass concurrently declined or increased during the same period.

Rosenberg et al. (2019) is a recent, influential study in avian conservation that demonstrates how traditional abundance-based approaches are being used to study birds at a macroecological scale. By estimating abundance changes to the North American bird community at large, the authors found a decline of three billion birds (29%) from 1970 to 2017. In a secondary analysis, the authors find a smaller 13.6% decline in the biomass of nocturnal migratory species during the same period (Rosenberg et al. 2019), but do not estimate biomass changes among non-migratory or diurnal migrant species. While abundance metrics tell one – albeit vital – portion of the story, understanding trends in species, trophic group and community-level biomass across the entire North American avifauna could provide important context for ecological conservation. Here, we extend the analysis of Rosenberg et al. by estimating avian biomass change in comparison to widespread abundance declines among North American birds and investigate how these changes manifest across trophic niche groups and breeding biomes.

Material and methods

We augmented abundance analyses conducted by Rosenberg et al. by multiplying estimated species-level abundance trends from 1970 to 2017 while accounting for uncertainty, by species' average mass estimates from AVONET (Rosenberg et al. 2019, Tobias et al. 2022). To do this, we first rerun the section of the analysis that produces yearly, species-level abundance estimates via a Bayesian hierarchical modeling approach using abundance data and population estimates from a variety of sources, including the USGS Breeding Bird Survey (Sauer et al. 2013), Audubon Society Christmas Bird Count (National Audubon Society 2023), and Partners in Flight (Stanton et al. 2019), among others. We then resampled from model-generated yearly abundance estimates ($n = 1000$) for each species and multiplied by the species' average mass estimate to calculate yearly, species-level biomass estimates over the study period. Using this approach, we were able to estimate biomass trends across species, groups, and the continental avifauna while propagating associated uncertainty in demographic trends.

Simultaneously, we categorized species by various traits to estimate biomass trajectories at the group level. For native and introduced species, we used classifications provided by Rosenberg et al. (2019). Species were grouped by trophic niche using classifications following Pigot et al. (2020) and AVONET (Tobias et al. 2022). All study species were assigned to one of ten groups based on resource use: frugivore, granivore, nectarivore, terrestrial herbivore, aquatic herbivore, invertivore, vertivore, aquatic predator, omnivore or scavenger. Species were also grouped by breeding biome classifications detailed in Rosenberg et al. (2019). By propagating uncertainty through species-level estimates, we could obtain estimates with associated uncertainty at the group-level.

During our analysis, we found two pairs of duplicate mass entries in the AVONET database for Canada goose/cackling goose *Branta canadensis*/*Branta hutchinsii* and Brandt's cormorant/pelagic cormorant *Urile penicillatus*/*Urile pelagicus* that appeared to be entered erroneously. For these four species, we recalculated the masses by averaging measurements in the source material cited in AVONET (Dunning 2007). As a result, two species mass estimates used in this analysis were revised to be higher than those reported in AVONET (Canada goose, Brandt's cormorant), and two were revised to be lower (cackling goose, pelagic cormorant). The revision of these mass values had no substantial impact on the results.

Results

Overall, we found that divergent trajectories in total biomass across trophic niche groups have led to an overall net increase in biomass of 11% (95% credible interval, CrI, 4–24%) despite abundance declines of 29% from 1970–2017 (CrI = −30 to −27%, Fig. 1–2A). Starting in 1970, overall biomass declined before reaching a local minimum in the 1990s, after which it increased dramatically, surpassing 1970 levels (Fig. 2A). Net biomass increases were the result of increases among six trophic niche groups (terrestrial herbivores, omnivores, scavengers, vertivores, aquatic herbivores and frugivores), offsetting the declines of four groups (invertivores, granivores, aquatic predators, nectivores, Fig. 1). One group, omnivores, had a substantial decline in abundance (−33%, CrI = −36 to −31%) but an increase in net biomass (18%, CrI = 8% to 29%). Despite this trend, two omnivorous species often thought to be highly adaptable, herring gull *Larus argentatus* and common crackle *Quiscalus quiscula*, represented two of the greatest single-species biomass declines (Fig. 3). Overall, gains in biomass were largely the result of increases among native species (17%, CrI = 8–31%), with introduced species declining (−31%, CrI = −39% to −20%). One species, the small (30 g) house sparrow *Passer domesticus* represented the second greatest decline in biomass across all North American species (Fig. 3). Across breeding biomes, net avian biomass increased in the arctic tundra (87%, CrI = 27–194%), among forest generalists (81%, CrI = 62–104%), and in wetlands (41%, CrI = 13–84%), with decreases in all other biomes (Fig. 2B). Increasing biomass can largely be explained by the recovery of many large-bodied birds (e.g. geese, vultures and wild turkey *Meleagris gallopavo*; Fig. 3) offsetting increases in certain human-associated species (e.g. common raven *Corvus corax*; Eurasian-collared dove *Streptopelia decaocto*).

Discussion

The trends observed for avian biomass and abundance in North America over nearly 50 years illustrate that across many avian species and large spatial scales, these two metrics can diverge dramatically. Given this, and the understanding that biomass metrics can be indicators of ecosystem function, we suggest that biomass is worthy of separate consideration by conservation biologists and managers when assessing ecosystem changes in response to climate change and other anthropogenic pressures. Our results suggest that North American avian communities are undergoing a complex restructuring of their composition, leading to an overall increase in biomass at the continental scale despite abundance declines among most species. The divergent trends observed can largely be explained by the increasing abundance of some of the largest species (e.g. waterfowl and vultures) occurring concurrently with losses among small species (e.g. flycatchers and warblers). Among the trophic niche groups considered, invertivores and granivores declined the most in biomass terms and now make up a substantially smaller fraction of the total avian biomass, aligning with other studies (Sauer et al. 2017, Spiller and Dettmers 2019). Overall, our results indicate that North American ecosystems support more avian biomass in 2017 compared to 1970, but the consequences of this complex restructuring in the context of net abundance declines are currently unknown and will require a multidisciplinary effort spanning population, community and ecosystem ecology.

Increasing biomass trends among North American birds can largely be explained by the successes of ongoing conservation efforts of large species, the unintended results of other anthropogenic activities, and may parallel increases in net global primary productivity (Hicke et al. 2002). Our

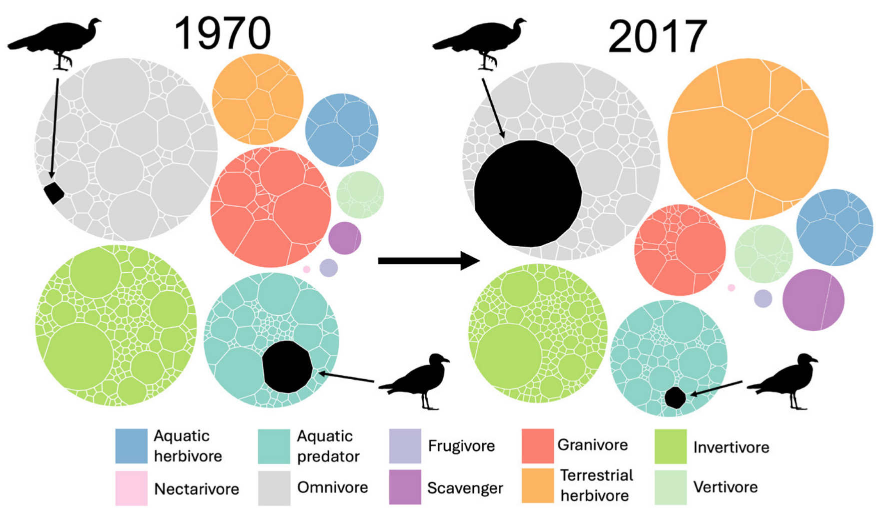

Figure 1. Biomass contributions of species (white-outlined inner shapes) nested within trophic niche groups (larger conglomerate circles) in 1970 and 2017. The size of internal shapes and larger circles represent relative contribution to total continental biomass. The species with the largest increase (wild turkey, *Meleagris gallopavo*) and decrease (herring gull, *Larus argentatus*) in biomass during the study period are highlighted in black.

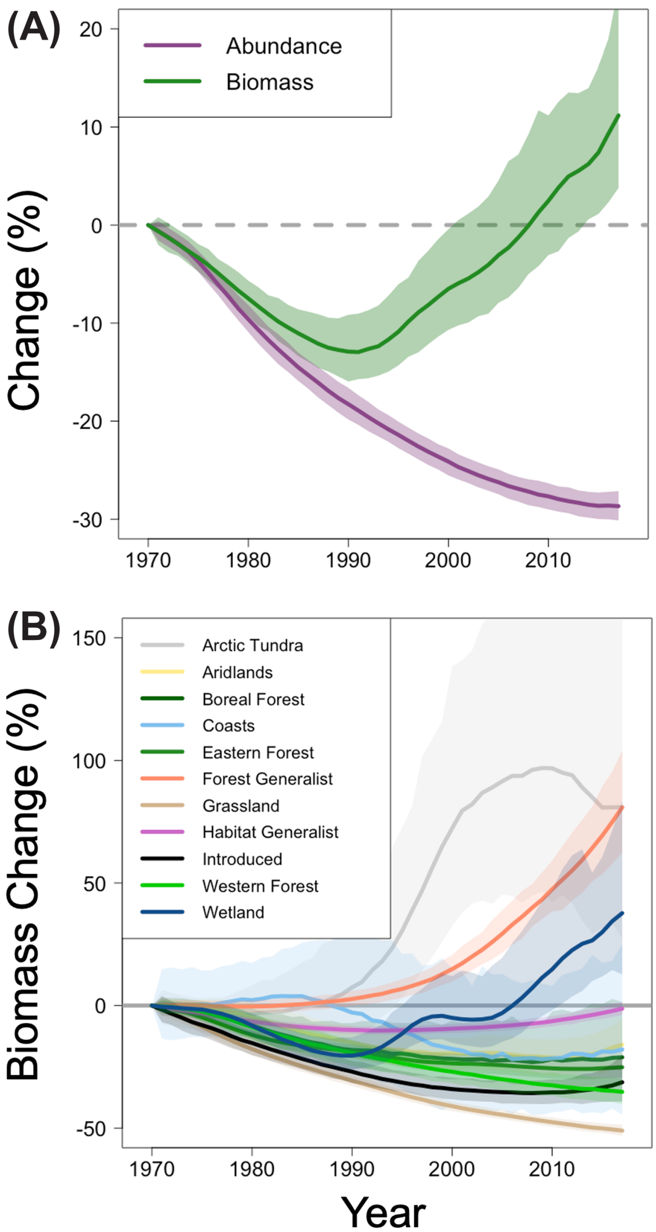

Figure 2. Abundance and biomass show diverging trends among North American birds. While mean abundance estimates (A, purple line with 95% CrI) decreased monotonically during the study period resulting in a 29% decline, biomass (A, green line with 95% CrI) increased by 11%. Biomass trends across breeding biomes were highly variable, increasing dramatically among arctic tundra and wetland birds, and among forest generalists (B), but decreasing in all other biomes.

findings specifically demonstrate that the increases in abundance among large gamebirds and waterfowl documented by Rosenberg et al. (2019) have had outsized energetic consequences. Increases across these groups have largely resulted from decades of targeted conservation and legislation (e.g. 1918 Migratory Bird Treaty Act), and an increase in applied environmental conservation (Sands and Pope 2010, Hudson et al. 2017, Anderson et al. 2018). For example, the continental biomass of wild turkeys has greatly increased from 2038 to 68 334 metric tons from 1970 to 2017. Wild turkeys represented an estimated 11% of the entire North American bird biomass in 2017 despite only representing a meager 0.2% of the continental avifauna abundance. Waterfowl are the second biggest positive contributors to increasing biomass trends, with many species' populations increasing dramatically. Snow goose *Anser caerulescens* and Canada goose populations, which represent the second and third largest contributors to continental avian biomass increases, have likely been buoyed not only by regional and federal waterbird conservation efforts, but by changing agricultural practices that unintentionally act as large-scale supplemental feeding operations (Abraham et al. 2005) increasing from a combined 1% of continental biomass in 1970 to 11% in 2017. Scavengers have similarly increased, likely due to decreasing pressure from human persecution and poisoning from DDT (Kiff 2000). Furthermore, an increase in plant productivity further north (O'Sullivan et al. 2020) may be beneficial to these species by increasing food availability, particularly on their breeding grounds. This trend towards the increased relative contribution of large-bodied birds to continental biomass means that substantial energy is being converted from plant and insect biomass to a few bird species, likely with profound ecosystem-level impacts. These shifts could have negative effects on other bird species if they reduce biomass available for consumption (i.e. by increasing competition), but could have little effect if the increased biomass consumption is coming from resources previously under-utilized, at least by birds.

Although biomass increases amongst gamebirds and waterbirds is certainly reflective of contemporary successes in conservation, the upward trajectory of biomass in other communities and trophic groups does not necessarily indicate that certain subsets of species are faring better compared to historical baselines. At the start of the study period, widespread pesticide use had caused the collapse of many species' populations (Fry 1995), and overexploitation following European colonization had already caused massive population declines and even extinctions of large-bodied, ecologically-important birds like the heath hen *Tympanuchus cupido cupido*, Carolina parakeet *Conuropsis carolinensis* and passenger pigeon *Ectopistes migratorius* (Smith et al. 2021). Before going extinct in 1914, the total biomass of the continent's three billion passenger pigeons (Schorger 1955, Hung et al. 2014) – weighing approximately 341 grams on average (Eaton 1910) – would have been more massive than the estimated biomass of the entire avian community of North America in 2017 (1 023 000 metric tons compared to 614 802). Although the current trajectory of continental biomass may be a positive development, it is important to note our results do not suggest that avian communities have recovered from intense post-colonial anthropogenic impacts. Estimates of historical biomass baselines could help conservation practitioners put the contemporary status and trends of energy flux and ecosystem functioning in perspective.

Avian conservation efforts currently focus on monitoring bird abundance and diversity. We suggest that conservation

Species	Mass (kg)	Abundance change	Biomass change (metric tons)
Wild Turkey (*Meleagris gallopavo*)	5.79	+11,447,518	+66,297
Snow Goose (*Anser caerulescens*)	2.64	+12,953,628	+34,148
Canada Goose (*Branta canadensis*)	3.73	+7,868,331	+29,327
Turkey Vulture (*Cathartes aura*)	1.94	+7,070,693	+10,734
Cackling Goose (*Branta hutchinsii*)	1.52	+4,144,905	+8,041
Eastern Meadowlark (*Sturnella magna*)	0.09	-73,943,124	-6,788
Thick-billed Murre (*Uria lomvia*)	0.96	-8,978,352	-8,655
Common Grackle (*Quiscalus quiscula*)	0.11	-82,867,155	-8,718
House Sparrow (*Passer domesticus*)	0.03	-330,908,461	-8,769
Herring Gull (*Larus argentatus*)	1.09	-10,508,755	-11,465

Figure 3. Species with the largest estimated increases and decreases in species-wide biomass during the study period (1970–2017). Overall biomass change may not reflect the product of mass and abundance change values due to rounding of species mass estimates. Species icons are not to scale.

biologists interested in ecosystem- or community-level change could complement these metrics by also monitoring biomass trends, without undue additional effort, thanks to the development of a comprehensive database of average weights for all bird species (Tobias et al. 2022). Bird biomass trends could be analyzed by dietary or trophic groups to inform questions related to ecosystem function and trophic dynamics, in tandem with abundance and biodiversity metrics to investigate whether biotic interactions are behind declines of species of concern. For example, net abundance declines concurrent with net biomass loss among granivorous birds in a grassland wildlife refuge could be interpreted as a sign of ecosystem collapse. In the same system, net abundance declines with steady levels of granivore biomass could indicate that some species are gaining ground at the expense of others, but that energy transfer and productivity, agnostic to species identity, is still being retained in the ecosystem. As has been suggested for other taxa (Saint-Germain et al. 2007), more monitoring, reporting, and simultaneous investigation of both abundance and biomass trends at varying spatial scales could provide a richer understanding of community turnover and changes to ecosystem function.

Conclusion

Through a re-examination of an important paper in avian ecology and conservation, we show that complementing traditional abundance-based research with biomass as a metric of interest can provide an additional energetics-based measure of ecosystem status. Incorporating biomass estimates into analyses can be relatively straightforward and useful at many different spatial, temporal, and taxonomic scales, but especially when assessing changes to community structure over time. Framing ecological and conservation questions with biomass in mind puts additional emphasis on changes in community structure, energetics and function, which can also be important considerations or even targets for conservation efforts. In short, considering biomass in tandem with metrics like abundance and biodiversity can help us achieve a richer understanding of the status of avian communities and their broader role in ecosystems.

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Author contributions

All authors contributed equally to this publication. **Benjamin A. Tonelli**: Conceptualization (equal); Formal analysis (lead); Writing – original draft (equal); Writing – review and editing (equal). **Joanna X. Wu**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Graham A. Montgomery**: Conceptualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are archived via Zenodo: https://doi.org/10.5281/zenodo.15319604 (Tonelli et al. 2025) and available on Github at https://github.com/bentonelli/North-American-Bird-Biomass.

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