

# Introduction

Understanding the interrelated dynamics of size- and -abundance based dimensions of biodiversity is key to understanding biodiversity change in the Anthropocene. Total abundance - i.e. the total number of individual organisms present in a system - and size-based currencies, such as the total biomass or total metabolic flux (“energy use”) of a system, are intertwined, but nonequivalent, measures of biological function. Abundance is more closely tied to species-level population dynamics, while size-based metrics more directly reflect assemblage-level resource use and contributions to materials fluxes at the broader ecosystem scale (Morlon et al. 2009, Dornelas et al. 2011, Connolly et al. 2005, White et al. 2007). While these currencies are naturally linked (Morlon et al. 2009, Henderson and Magurran 2010), changes in size composition can decouple the dynamics of one currency from another (Ernest et al. 2009, Dornelas et al. 2011, White et al. 2004, 2007, Yen et al. 2017). This can mean that intuition from one currency may be misleading about others; a trend in numerical abundance might mask something else going on with biomass (White et al. 2004). Changes in size composition strong enough to decouple currencies may be symptomatic of important changes in ecosystem status- e.g. abundance-biomass comparison curves (Petchey and Belgrano 2010); size-biased extinctions (Young et al. 2016, Smith et al. 2018). This underscores the need to understand how these dynamics are playing out in the Anthropocene (Fisher et al. 2010).

At the community scale, changes in the relationship between size and abundance can signal important shifts in community structure and functional composition. To the extent that size is a proxy for other functional traits, changes or consistency in the community-level size structure (individual size distribution, ISD) over time may reflect processes related to niche structure (White et al. 2007, Petchey and Belgrano 2010). Strong size shifts can decouple the relationship between abundance and biomass. In aquatic systems, such changes in the scaling between abundance and biomass often signal ecosystem degradation (Warwick and Clarke 1994 and refs therein, Kerr and Dickie 2001, Petchey and Belgrano 2010). Compensatory shifts in the size structure can buffer community function (in terms of biomass or energy use) against changes in abundance (Ernest et al. 2009, White et al. 2004, Terry and Rowe 2015). Consistency in the size structure may maintain the relationship between size- and -abundance based currencies, even as species composition, total abundance, and total biomass/total energy use fluctuate over time, which can reflect consistency in the niche structure over time (Holling 1992).

It is important to improve our understanding of these dynamics for terrestrial animal communities in particular. In contrast to terrestrial trees and aquatic systems (Kerr and Dickie 2001, White et al. 2007), how the relationship between size and abundance changes over time, and the consequences of these changes for ecosystem-level properties, remain relatively unknown for terrestrial animals (but see White et al. (2004)). Terrestrial animal communities exhibit size structure (Thibault et al. 2011, Ernest 2005), and case studies have demonstrated that size shifts can decouple the dynamics of abundance, biomass, and energy use for terrestrial animals (White et al. 2004, Yen et al. 2017), but do not always do so (Hernández et al. 2011). Establishing generalities in these dynamics is especially pertinent in the Anthropocene, as these communities are experiencing extensive and potentially size-structured change, with implications at community, ecosystem, and global scales (Young et al. 2016, Schmitz et al. 2018).

Macroecological-scale synthesis on the interrelated dynamics of the ISD, total abundance, and community function for terrestrial animals has been constrained by 1) a lack of community-level size and abundance timeseries data for these systems (Thibault et al. 2011, White et al. 2007), and 2) appropriate statistical methods for relating change in the size structure to changes in abundance and function (Thibault et al. 2011, Yen et al. 2017). In contrast to aquatic and forest systems, most long-term surveys of animal communities do not collect data on individuals’ *sizes* across a full community (with the exception of small mammal studies, which have made major contributions to our understanding of the dynamics of size, abundance, and function for these systems; (White et al. 2004, Ernest 2005, Hernández et al. 2011, Kelt et al. 2015)). Global, continental, or population-wide studies capture different phenomena (White et al. 2007, McGill et al. 2015). The ISDs for terrestrial animals, and specifically for determinate growing taxa (e.g. mammals, birds), are often complex, multimodal distributions (Holling 1992, Thibault et al. 2011, Ernest 2005, Yen et al. 2017), and less statistically tractable than the power-law ISDs found in aquatic and tree systems (Kerr and Dickie 2001, White et al. 2007). Quantifying change in the size structure, and relating this to change

in community-wide abundance and function, is not as straightforward as computing and comparing slopes. As a result, we do not have a general understanding of either 1) how these ISDs behave over time or 2) the extent to which changes in the ISD decouple the community-level dynamics of abundance, biomass, and energy use in these systems.

Here, we begin to address this gap by exploring how temporal changes in species composition and the size spectrum modulate the relationship between total abundance, energy, and biomass for communities of North American breeding birds. We used allometric scaling to estimate community size and abundance data for the North American Breeding Bird Survey, and evaluated how changes in total abundance, biomass, and energy use have co-varied from 1988-2018. Specifically, we examined: 1) How often do these currencies change together vs. have decoupled dynamics?; 2) What are the dominant directions and magnitudes of the overall change and any decoupling between the currencies?; 3) To what extent do changes in the ISD translate into decoupling between abundance and function?

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