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Biodiversity–ecosystem function research must consider abundance and not just diversity

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Maintaining human well-being in an era of biodiversity loss requires understanding the role of biodiversity in ecosystem function. We argue that absolute abundance can drive ecosystem function and that this measure should be considered alongside traditional measures of biodiversity.

Researchers who investigate the relationship between biodiversity and ecosystem function typically use the number of species (species richness), or diversity metrics that combine species richness with relative abundances (evenness), as the measure of biodiversity. Hundreds of biodiversity–ecosystem function experiments have shown that various types of ecosystem functions increase with these biodiversity measures[1]. However, in naturally assembled communities studied at larger spatial scales, the findings are mixed; species richness is not always found to be associated with greater ecosystem function[1–4]. The focus on species richness neglects the importance of another main driver of ecosystem function: absolute abundance, or simply the number of individuals present. Here, we discuss how and why abundance has been previously neglected in this field, and argue that its consideration could provide a more accurate view of the potential change in function when species decline in both abundance and diversity.

Ecological experiments usually assemble seminatural communities while trying to control the total abundance of the organisms that provide the function. But in the real world, abundance varies substantially across space, which has consequences for key ecosystem functions such as pest control, seed dispersal and pollination[5]. For example, the abundance of pollinators can vary greatly across sites, and sites with high total abundance can have high levels of pollination function regardless of species richness (Fig. 1). Well-intentioned experimental design choices in biodiversity–ecosystem function research might underestimate the role of abundance in driving ecosystem function in natural settings.

Even in observational studies, most measurements of biodiversity as a predictor variable explicitly exclude absolute abundance[6]. Specifically, the Shannon index, the Simpson index and Hill numbers all normalize by aggregate abundance, and thus retain information about only the relative — and not the absolute — abundance of each species[7]. These metrics make the effect of absolute abundance on ecosystem function undetectable, even if it is present in the data. Furthermore, species richness can correlate with absolute abundance for both artefactual and biological reasons; the number of species detected increases with the number of individuals in the sample[7], and locations with more resources can support both more individuals and more species. Thus, the exclusion of absolute abundance from many biodiversity–ecosystem function analyses means it could be a confounding variable behind some of the published findings that show that ecosystem function increases with increasing species richness.

The origins of biodiversity–ecosystem function research might explain, in part, why absolute abundance has been neglected. Grassland plants were the first experimental system used to test biodiversity–ecosystem function relationships and they continue to be a main model system for both experimental and observational studies[2,4]. However, determining what counts as an individual grassland plant can be challenging because many species spread vegetatively and have indeterminate growth. Thus, grassland plant studies rarely report the abundance of each species that contributes to the ecosystem function. Biomass per species is an alternative measure of abundance, but it is rarely used as a predictor variable. Instead, biomass, or the related variable productivity, is traditionally used as the outcome variable (in other words, the ecosystem function). These features of the standard model system might have contributed to the omission of absolute abundance (or biomass) as a predictor variable in biodiversity–ecosystem functioning research generally.

Given these omissions, direct evidence that absolute abundance drives ecosystem function is sparse. That said, numerically dominant species have been found to deliver most of the ecosystem function in some settings. For example, 1% of the tree species in the Amazon Basin store 50% of the carbon[8], and 17% of the bee species at farms in California provide 80% of the pollination[9]. Ecological communities almost always have a few numerically dominant species, each represented by many individuals, and many rare species, each represented by only a few individuals[10]. If the amount of a function a species provides generally follows from its abundance[11], logic suggests that most of the function should be provided by a few abundant species. Surprisingly, the extent to which this pattern is the general case in nature is unknown[10].

To make progress, ecology needs more studies that measure the ecosystem function provided by every species in a community, so that general conclusions can be drawn about the functional importance of numerically dominant species. More broadly, ecology needs more biodiversity–ecosystem function studies that measure the number of individuals and then include absolute abundance as a predictor variable in the analysis. This measurement might be easier for animals than for plants. Spatial scale will be important to consider in these studies as well, because the identity of the dominant species varies across space, such that the total number of species that are dominant somewhere accumulates with the spatial scale examined[12].

Considering the importance of species abundance is critical, given the pace at which wild biomass is decreasing. Indeed, since the rise of

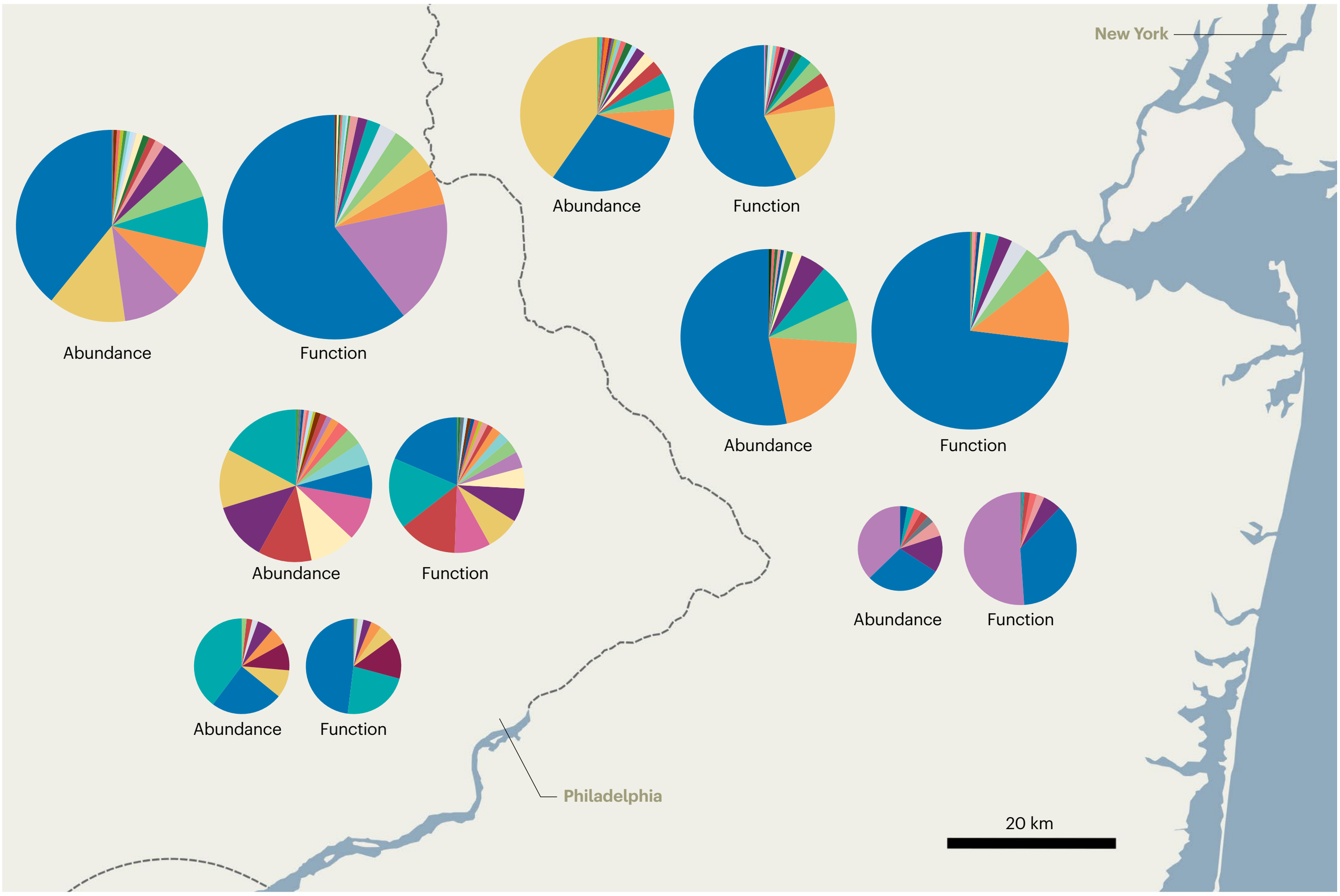

Fig. 1 | An illustrative example of how absolute abundance can drive ecosystem function. In these data (from ref. 12) on wild bee communities that pollinate watermelon crops, the pie charts show the abundance (total number of individual bees; left-hand pies) and pollination function provided (number of watermelon pollen grains deposited; right-hand pies) by different bee species (wedge colours) at six sites. Abundance varies markedly across these real-world sites and this variation is not captured by ecologists' traditional diversity metrics.

humans, the global biomass of wild animals has declined by 83%, and that of plants by 50%[13]. Importantly, abundance could be declining more rapidly than species richness because population size declines long before a species becomes locally or globally extinct. Species richness is not, in fact, decreasing at local scales[14]. Thus, concluding that ecosystem function relies only on local species richness could lead erroneously to the prediction that ecosystem functions are currently being maintained at suitable levels. Conversely, if absolute abundance measurably affects ecosystem function, ongoing declines in biomass could mean that many functions and services important to humans are being lost. It is time to find out.

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Competing interests

The authors declare no competing interests.