Biotic impoverishment

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Predicting how biotic impoverishment impacts ecosystem processes requires a multidimensional approach

A central goal of ecologists today is to be able to predict the environmental consequences of humanity's alteration of life on Earth. We have changed our world so much that many propose considering the Holocene officially over and naming this new epoch in Earth's history the Anthropocene (Crutzen, 2002; Zalasiewcz et al., 2008). Several features distinguish the Anthropocene from the Holocene, but changes in the diversity of life are among the most prevalent. These include:

- the absence of megafauna species once common in the Pleistocene now extinct in part because of human hunting (Barnosky et al., 2004),
- the increasing loss of top predators and other apex species (Estes et al., 2011),
- the rise of agriculture that now covers 40% (Ramankutty et al., 2008) to 75% (Krausmann et al., 2013) of the vegetated surface of Earth,
- a 10–100 fold increase in extinction rates that is propelling us towards a sixth mass extinction (Barnosky et al., 2011),
- and the likely collapse of most of our fisheries in the next 50 years (Worm et al., 2006).

The biosphere has clearly undergone, and is undergoing, an unprecedented biotic change. From a Holocene world made up of about 10 million species (Mora et al., 2011), we are moving to an Anthropocene world dominated by one species (our own), 35 species of livestock, and 30 crop species (FAO, 2013). The remaining terrestrial species live on land of substantially lower productivity than the land we have appropriated (Haberl et al., 2004). Marine species are even worse off. Our oceans are polluted, acidifying, and shifting in trophic composition as top predator species are overfished (Jackson, 2008). The Anthropocene is a novel biological realm.

One way to approach the problem of understanding the significance of biotic change is to compare characteristics of two or more replicates of unit spaces which contain different biota. To illustrate, let us first consider the biosphere of the Holocene versus that of the Anthropocene. In virtually any space on Earth's surface whose physical and chemical conditions are conducive to life, microbes and most likely plants and animals will be found. Their presence alters the fluxes of energy, elements and materials through this space. We need to figure out what the average amount of biomass is per unit space which means we need to estimate the total global biomass and divide that by an estimate of the total volume of habitable space on Earth.

We can estimate the total volume of habitable space, or the volume of the biosphere, by considering the extremes of where life is found. A snail fish, for example, has been found on the ocean floor at a depth of nearly 8 km (Jamieson et al., 2009), well below the average ocean depth of 3.68 km (Charette and Smith, 2010). The estimated ocean volume, which is based on the product of the surface area of the ocean and the average depth, is 1.33 billion cubic kilometers (1.4×10^9 km^3, Charette and Smith, 2010). A vulture was found flying 11 km above sea level (Laybourne, 1974), so we can estimate the volume of habitable space over land by multiplying the total area of land (i.e., 150×10^6 km^2) by 11 km, which yields 1.65×10^9 km^3. Add these estimates for the volume of habitable ocean and the volume of habitable space above land and the volume of the biosphere appears to be about 3 billion cubic kilometers (or 3.0×10^9 km^3).

The estimated total mass of life occupying this space, using carbon content as our measure, is enormous — approximately one trillion tons or 1.0×10^{12} t C (Whitman, Coleman and Wiebe, 1998).

Returning to our original problem of estimating the average amount of biomass is per unit space, we get Global biomass C/volume of habitable space on Earth $\approx (1.0 \times 10^{12} \text{ t C})/(3.0 \times 10^{9} \text{ km}^3) = (1.0 \times 10^{21} \text{ mg C})/(3.0 \times 10^{21} \text{ l}) = 0.33 \text{ mg C l}^{-1}$.

Given this enormous mass of biomass, it is not surprising that gigatons (i.e., billions of tons) of biologically important elements such as carbon, nitrogen, phosphorus, and sulfur move annually between land, ocean, and atmosphere. These biologically-driven geochemical, or *biogeochemical* processes, are what make Earth habitable (Schlesinger and Bernhardt, 2012). What *is* surprising, however, is that if a liter of the biosphere, on average, contains just 0.33 mg of biomass (again, in terms of C) per liter. So while a trillion tons of biomass sounds like a lot, on a per-unit space, the biosphere is rather thinly diffused with life. Thin though it is, it is dense enough to transform Earth from a lifeless planet to a vibrant, dynamic, and productive home for ourselves and millions of other species.

We can now compare the average properties of a unit space of the Anthropocene biosphere with the Holocene biosphere. The question we would ask is whether a spatial unit of the Holocene biosphere changes in its biogeochemical functioning if its biota changes. If the average biomass content of the unit (i.e., 0.33 mg per liter) declined, we might guess that the magnitude, rate, and stability of its biogeochemical functioning would all decline. The question that is more germane, but much more difficult to address, is if the biomass content of the unit remained constant at 0.33 mg C per liter, but the average biodiversity in a liter declined, do the magnitudes, rates, and stability increase, decrease, or remain unchanged?

The idea of an ecological unit is admittedly abstract, but it illustrates the primary objective of research focused on the environmental consequences of biotic impoverishment. Unlike the term *biodiversity loss*, which usually refers to the local or global extinction of species, biotic impoverishment refers to any decline in biodiversity per unit of ecological space. While extinction certainly makes biotic impoverishment worse, even if no species went extinct, biotic impoverishment could still occur. For example, if the unit of ecological space experienced a decline in

- taxonomic diversity,
- phylogenetic diversity,
- functional diversity,
- genetic diversity,
- genomic diversity,
- trophic diversity,
- interaction diversity,
- spatial or temporal diversity (e.g., a change in composition over space or time),

or any other dimension of biodiversity (see Common dimensions of biodiversity, below, for descriptions of these dimensions of biodiversity), but the number of species remained constant, biotic impoverishment would still occur (Naeem, Duffy and Zavaleta, 2012).

In the abstract exercise above, the spatial unit (i.e., 1 liter) was for the entire biosphere. More practically, given Earth's heterogeneity that ranges from icy poles and tropical forests to dark oceanic abysses and coral reefs, we would work at smaller scales and then scale up. We would work at the scale of the biome, landscape, ecosystem, or, experimentally, at the level of a field plot or laboratory mesocosm or microcosm.

The study of biodiversity and ecosystem functioning (BEF) explores the environmental consequences of biotic impoverishment in the Anthropocene by comparing spatial units of the biosphere that vary in biodiversity. The central idea is to consider how biodiversity per unit ecological space functions under Holocene levels of diversity, which are presumed to be very high, compare with Anthropocene levels, which are presumed to be very low. For example, the first BEF study, conducted in 1992, built fourteen replicate spatial units of an old-field ecosystem in growth chambers that had identical light regimes, nutrient abundance, water inputs, air flow, and soil volume (Naeem et al. 1994). However, the number of species and interactions were deliberately varied between high (e.g., Holocene), intermediate (e.g., Anthropcene), and low (e.g., future) levels of biodiversity. The study found that simultaneously changing taxonomic and interaction diversity significantly affected carbon dioxide flux, nutrient flux, and other biogeochemical processes, even though the initial conditions of the units were all the same. Biodiversity was simply indexed as high, intermediate, and low and ecosystem functions were considered to be processes that concerned energy and material flow through the 8 m³ ecological space (i.e., the growth chamber). Prevailing hypotheses at the time ranged from biotic impoverishment having no effect to having dramatic effects on ecosystem functions. This first study suggested that it was the latter — almost all ecosystem functions in the high diversity replicates (i.e., the Holocene replicates) were significantly different from the intermediate and low diversity replicates (e.g., the Anthropocene replicates). This single mesocosm study, however, was insufficient to shed much light on the question and perhaps generated more discussion than convinced any one that the Anthropocene was going to be significantly different from the Holocene in the face of biotic impoverishment.

Why did changing biodiversity in a unit ecological space lead to higher levels of ecosystem functioning in this experiment? The study argued that greater biodiversity enhanced magnitudes of functioning because more diversity meant greater likelihood that species would collectively make more efficient use of energy and
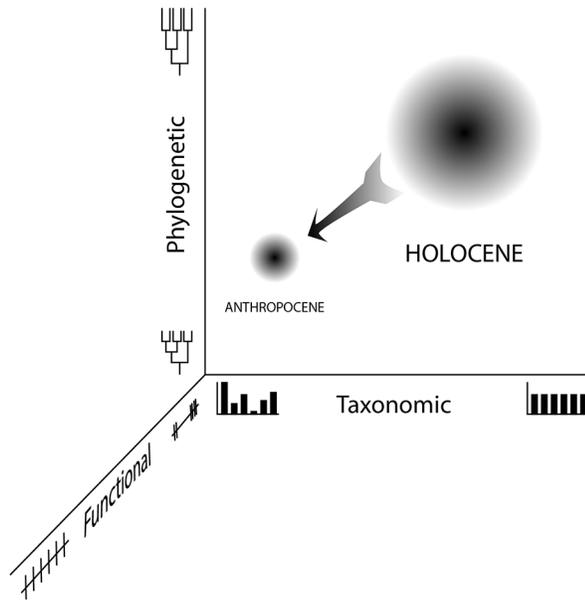
resources available in the unit space than single species could do alone. The classic example is that neither shallow- nor deep-rooted plant species make efficient use of soil compared to both working together. Meta-analyses of BEF experiments support this mechanism for many studies, but not all (Cardinale et al., 2006).

Now, some 20 years and over a thousand studies later, the impacts of biotic impoverishment on ecosystem functioning are relatively clear (Cardinale et al., 2012; Naeem, Duffy and Zavaleta, 2012). BEF studies have ranged from laboratory microcosms of bacteria to replicated field plots of vegetation to observational studies of nature *in situ*. Though impacts of biotic impoverishment in these studies varied from nil to significant depending on the ecosystem, the ecosystem functions measured, and the nature of the changes in biodiversity, biotic impoverishment can clearly alter the magnitude, efficiency, and stability of multiple functions (e.g., primary production, nutrient cycling, carbon flux, invasion resistance, resistance to the spread of diseases, and pollination efficiency). Variation in how researchers define and measure ecosystem functions makes comparing studies difficult. For example, many researchers consider plant or primary production an ecosystem function and quantify it as above ground biomass while others measure both above- and belowground biomass. Other studies are more specific, focusing on single steps in a nutrient cycle, such as N mineralization, while other studies measure abstract properties of an ecosystem, such as the ability to resist invasion by exotic species or by disease organisms. In general, in spite of the rich variety of definitions and methods of quantification of ecosystem functions, the overall consensus is that most ecosystem functions examined, singly or collectively, have proven to be sensitive to changes in one or more dimensions of biodiversity (Cardinale et al., 2012).

While no study has attempted to scale up BEF findings to the biosphere, the body of literature is robust enough for the scientific community to extrapolate to large scales and suggest basic principles and likely impacts on human wellbeing in the Anthropocene (Cardinale et al., 2012). Experimental studies have ranged from manipulating bacterial diversity in micro-well plates using robotic pipettors (Wittebolle et al., 2009) to hand planting mixtures of grassland plants across hundreds of field plots (e.g., Isbell et al., 2011). Observational studies have examined long-term trends in the grasslands of Inner Mongolia (Bai et al., 2004) to salmon populations in Bristol Bay, Alaska (Schindler et al., 2010). Collectively, these studies of biotic impoverishment suggest that the Anthropocene biosphere could be less biogeochemically active, lower in efficiency (lower biogeochemical functioning per unit energy and nutrients consumed), and less stable (Fig. 1). That sounds scary, given that 7 billion people count on the biosphere to provide them with food, water, and a safe planetary abode (Rockstrom et al., 2009), but now are facing an impoverished, shaky, unpredictable world. It remains both an interesting and also incredibly important question whether we can predict how biotic impoverishment is likely to change our biosphere.

There are a number of exciting frontiers in the field of biodiversity and ecosystem functioning, but none are as challenging as considering the multiple dimensions of biodiversity. While most studies have focused on taxonomic diversity (Zavaleta et al., 2010; Morin et al., 2011; Paquette and Messier, 2011), other dimensions have increasingly come under investigation, including genetic (e.g., Hughes et al., 2008; Eisenhauer, Scheu and Jousset, 2012), functional diversity (e.g., McLaren and Turkington, 2011; Sekercioglu, 2012), interaction diversity (e.g., Connolly et al., 2011), and phylogenetic diversity (e.g., Cadotte, 2013), but few have explored multiple dimensions. Those that have, such as Flynn et al. (2011) and Cadotte, Cardinale and Oakley (2008), have provided greater insights into the mechanisms responsible for the influence of biodiversity on unit ecosystem functioning. The challenge is how to either conduct an experimental study or statistically analyze observational data to reveal how taxonomic, phylogenetic, genetic, genomic, functional, trophic, interaction, and perhaps other dimensions, such as spatial and temporal dimensions of biodiversity, simultaneously influence ecosystem functioning. There are also needs to determine what the baselines are for different dimensions of biodiversity and how different anthropogenic drivers affect each dimension. Such research borders on the completely intractable, yet it needs to be done because changes in each dimension of biodiversity affect ecosystem functioning in different ways.

This is an exciting and daunting phase in the study of biotic impoverishment. Technological advances are rapidly increasing methods for quantitatively assessing different dimensions of biodiversity. Remote sensing is developing ways to identify diversity in vegetation through hyperspectral analysis, DNA barcoding is accelerating biodiversity discovery, advances in computer and web-based technologies are allowing for the assembly, sharing, and integration of massive biodiversity databases, and theoretical and empirical studies of biotic impoverishment are growing exponentially. Most exciting are molecular advances, such as the GeoChip (e.g., He et al., 2010a; He et al., 2010b), that are allowing us to examine microbial diversity in ways that were never possible before (Zak, Blackwood and Waldrop, 2006). Such sequence- and gene-based methods, although data intensive, may also reduce the number of dimensions of biodiversity needed for a BEF study much the way phylogenetic diversity captures both taxonomic and functional diversity (Cadotte et al., 2008; Flynn et al., 2011). Important changes in the social dimension of the issue include the rise in Payment for Ecosystem Services as an economic instrument for promoting sustainable use of biodiversity and the services it provides (Farley and Costanza, 2010), the establishment of twenty Convention on Biological Diversity Targets to be achieved by 2020 (Perrings et al., 2010), and the establishment of the Intergovernmental Platform for Biodiversity and Ecosystem Services (Larigauderie and Mooney, 2010). Such activity on both social and

natural science fronts is encouraging, but progress will be contingent on our arriving at a better understanding of just what exactly an ecosystem's biological diversity is, in all its dimensions before we start to predict the consequences of its impoverishment. Maybe the biotically impoverished Anthropocene is a better place for humanity, maybe it is a worse place and needs to be managed differently — either way, modern research will help shed light on the issue.

Common dimensions of biodiversity

Most studies of biodiversity and ecosystem functioning focus on taxonomic diversity, though increasingly functional and phylogenetic diversity are being used. Other dimensions of diversity, such as trophic diversity and genetic diversity, are rarely examined.

- Taxonomic diversity — the number and relative abundance of taxa (e.g., species, genera, families, and onward)
- Phylogenetic diversity — relationships among taxa based on times since divergence (e.g., sum of the branch lengths linking species in a phylogeny)
- Genetic diversity — nucleotide, allelic, chromosomal, genotypic, or other aspects of genomic variability
- Genomic diversity — similar to genetic diversity but focused on sequence similarity or sequence variability of genomic elements such as single-nucleotide polymorphisms (SNPs), large-sequence polymorphisms (LSPs), or repetitive elements such as microsatellites, telomeres, and mobile elements
- Functional diversity — variation in the degree of expression of multiple functional traits
- Spatial or temporal diversity — rates of turnover of species through space or time
- Interaction diversity — characteristics of the network of interactions, such as competition, predation, parasitism, or facilitation, among species
- Trophic diversity — similar to interaction diversity but limited to trophic or feeding interactions such as predation, herbivory, and parasitism.

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