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**COMMENTARY**

# Revisiting the carbon–biodiversity connection

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The link between biodiversity and ecosystem function has long been a subject of intense interest and debate among biologists, going back to the time of Charles Darwin, whose ideas on species interactions presaged subsequent discussions of biodiversity and ecosystem function (Peterson et al., 1998). Since then, many considerations of community diversity have centered on the importance of species or functional diversity for maintaining system resilience in the face of disturbance, analogous to the way that interwoven threads maintain the function and integrity of fabric. While our language, concepts, and methods have evolved over time, a key question regarding diversity and function persists today: *What exactly is the link between biodiversity and ecosystem function?* With ongoing human activity altering many parts of the planet, an additional pressing question emerges: *How can we best manage ecosystems to enhance both biodiversity and biological carbon sequestration?*

In recent years, a growing number of studies have considered the co-benefits of biodiversity and carbon sequestration. Many of these have been experimental studies of grasslands where annual production is relatively easy to assess, and most of these studies have emphasized primary producers and above-ground yield (e.g., Fraser et al., 2015; Tilman, 1999). Similarly, most forest and cropland studies have focused on primary production with an emphasis on the relatively accessible above-ground component, without clearly addressing overall system biodiversity. While notable exceptions exist (e.g., Fraser et al., 2015), many of these biodiversity and ecosystem function studies report a positive association between biodiversity and biomass yield (e.g., Tilman, 1999), sometimes leading to the general conclusion that biodiversity begets productivity, or vice versa.

A counterargument can also be posited that highly productive ecosystems can be generated with intensively managed monocultures where cultural practices and resource inputs ensure high

yields (Silvertown et al., 2006). From the narrow standpoint of maximizing biological carbon uptake, this approach can seem attractive. However, while undoubtedly highly productive, intensively managed systems often come at great expense in terms of labor, energy, nutrient and water inputs, often with attendant economic and environmental costs, including the displacement of natural ecosystems, enhanced greenhouse gas emissions, and reduced water quality (Foley et al., 2011). These approaches fail to meet current biodiversity objectives and are generally less resilient than diverse ecosystems, calling into question the wisdom of engineered, single-species solutions. These significant negative externalities lead to a new question: *What are the overall, long-term costs and benefits of our ecosystem management choices regarding carbon and biodiversity?* Studying costs and benefits for complex ecosystems can be difficult, suggesting that simple answers to these questions will remain elusive. Rather than addressing these topics using experimental approaches that necessarily simplify the system and limit the measurements to a subset of species in highly managed conditions, can we find clear answers to these questions using relatively unmanaged natural ecosystems?

A recent study by Schuldt et al. (2023) has tackled these issues in a regenerating forest with remarkable results that deserve careful attention by all interested in the relationships between biodiversity and carbon. In a detailed exploration, the authors explore carbon–biodiversity connections with an extensive dataset on biodiversity and carbon stocks from a secondary subtropical forest in China (Gutianshan National Nature Reserve). The study is a tour de force, both for the depth and breadth of its analysis.

Unlike most studies limited to certain trophic levels and focusing primarily on above-ground carbon, Schuldt et al. (2023) considered the relationship between several ecosystem carbon components

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and multiple trophic levels spanning over 4600 species across 25 study plots. In their wide-ranging analysis, they considered: (1) dead and below-ground carbon in addition to above-ground carbon stocks, (2) mediation of the carbon–biodiversity relationship by a variety of heterotrophic organisms, and (3) dependence of conclusions about carbon–biodiversity links upon the trophic levels considered. The study also examined directional versus correlational analysis to see which perspective better depicts the relationships between diversity and carbon.

The study found that relationships between biodiversity and carbon stocks varied with the carbon stocks and trophic levels examined. Carbon–biodiversity linkages appear to be mediated by the diversity of resources, including deadwood and below-ground carbon, not simply by above-ground carbon stocks that are easily measured. Above-ground carbon stocks were not strongly related to biodiversity for most trophic groups, with the exception of saprophytic fungi. Total forest carbon emerged as a significant predictor of heterotrophic biodiversity, but this was primarily mediated by below-ground carbon, and not strongly related to above-ground carbon.

In their careful untangling of the complex web of relationships in a naturally regenerating forest, the authors addressed several challenges that have plagued previous studies focused on a few of the more visible threads in the fabric. The authors emphasize that most studies have been limited to certain trophic levels (particularly primary producers), and often with principal attention to above-ground portions of the community. The variation of the results depending upon which carbon stocks and trophic levels are examined remind us that ecosystem interactions are not always unidirectional cause and effect relationships, but multifarious associations involving complex feedbacks between system components, some of which are more accessible than others. The study argues against overly simplistic solutions to carbon management based on limited examination of the more visible trophic levels or above-ground carbon stocks only. These findings are consistent with other recent work indicating that natural ecosystem restoration provides a more effective solution to enhancing carbon sequestration than engineering highly productive but species-poor monocultures (Lewis et al., 2019). Biological sequestration solutions that do not consider the full costs and benefits of ecosystem management choices in a realistic way may be illusory.

This work serves as a cautionary tale for ongoing efforts to assess biodiversity and ecosystem function by using remote sensing, which is now widely employed for large-scale evaluations of both biological carbon sequestration and biodiversity. Remote sensing remains one of the few methods able to sample truly large areas while providing uniform coverage in a consistent format. Great strides are being made in the use of remote sensing for biodiversity assessments, leading to calls for a Global Biodiversity Monitoring System (Cavender-Bares et al., 2020). However, the view from above afforded by most remote sensing methods tends to limit such assessment to the more visible (above-ground) parts of primary producers rather than the below-ground components, often at overly coarse scales. Remote sensing alone cannot directly view the entire system

in the kind of fine detail needed for a full understanding of the interactions between biodiversity and ecosystem function. Such synoptic views allow us to see the general pattern of the cloth, but not the contribution of all the individual threads. Remote sensing often performs best when integrated with a full suite of independent field methods at finer scales, and the synergistic integration of remote sensing with well-designed field studies can enhance the effectiveness of both (Turner, 2014).

Schuldt et al. (2023) provides a compelling example for how such critical field studies might be done as we envision a Global Biodiversity Monitoring System integrating networks of field sites with multi-scale remote sensing campaigns around the dual themes of carbon and biodiversity.

The authors remind us that a full assessment of biodiversity–carbon links requires a careful evaluation of multiple carbon stocks, trophic levels, and their interactions; a simple approach that considers only above-ground stocks or only one taxonomic level might easily mislead us or engender inappropriate practices or policy conclusions. The work adds support to the mounting evidence that encouraging natural ecosystem restoration with a diversity of species, as opposed to planting highly managed monocultures, may best provide the essential co-benefits of carbon sequestration and biodiversity enhancement. Given the current critical challenges of declining global biodiversity and perturbed carbon cycles, we would all do well to carefully consider the findings of Schuldt et al. (2023).

#### CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed for the current article.

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