frontiers
in Ecology and Evolution

EDITORIAL
published: 01 May 2019
doi: 10.3389/fevo.2019.00144

Editorial: Revisiting the Biome Concept With A Functional Lens

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Keywords: biome, ecosystem function, functional traits, vegetation, evolutionary history

Editorial on the Research Topic

Revisiting the Biome Concept With A Functional Lens

Early biogeographers such as Alexander von Humboldt recognized the broad-scale coupling of vegetation and climate (von Humboldt, 1806). This observation shaped the modern biome concept which organizes ecosystems by assumed relationships to environmental controls. Biomes are essential constructs for understanding vegetation distributions, the evolutionary patterns that shape species pools (Crisp et al., 2009; Cornwell et al., 2014), and the environmental impacts of human activities (Olson et al., 2001; Mucina, 2019), among other applications. However, ecologists recognize that there are regions, especially in the tropics, where vegetation may not deterministically relate to climate (Whittaker, 1975; Staver et al., 2011; Moncrieff et al., 2015). The biome concept is operationalized in practice as a static classification of the land surface. Process models rely on these classifications to summarize vegetation into Plant Functional Types (PFTs) which form the basis for representing ecosystem function and biogeochemical rates. Recently this approach has been criticized for missing key impacts on the distribution and functioning of biomes like historical contingency, biogeographic history, disturbance ecology, and evolution (reviewed in Higgins et al., 2016; Pausas and Bond, 2018). Thus, further research is required to better define biomes based on species composition and phylo-functional diversity, as well as better understand the drivers of biome boundaries and functioning within and among biomes.

A new understanding of biomes is crucial for appropriate prediction of future environmental change and global biogeochemical cycle modeling based on highly abstracted PFTs (Higgins et al., 2016; Still et al., 2018). In this issue, we present synthetic research ranging from continental-scale biogeography of biomes (e.g., Echeverría-Londoño et al.; Pinto-Ledezma et al.) to functional assessments of individual dominant species (e.g., Bachle et al.). These studies combine functional data with species distributions and phylogenies to provide new insight into the nature of biomes and how we can best capture the functional impacts of unique biogeographic histories (e.g., rare long-distance dispersal Deng et al.). They also indicate a major need for field data to fill gaps in datasets and for model parameterization. Focusing on all of North and South America, Echeverría-Londoño et al. compare and contrast functional diversity across biomes. They analyze the distributions of over 80,000 plant species combined with functional trait data for an ∼8,000 species subset. They report a general relationship between species range size and functional distinctiveness. Rare species are functionally distinct, whereas common species are functionally similar within each biome.

Edited and reviewed by:
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Specialty section:
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

Received: *27 March 2019*
Accepted: *12 April 2019*
Published: *01 May 2019*

Citation:
Griffith DM, Still CJ and Osborne CP (2019) Editorial: Revisiting the Biome Concept With A Functional Lens. Front. Ecol. Evol. 7:144. doi: 10.3389/fevo.2019.00144

Extant ecosystem function is a product of the assembly processes that shape the structure of communities (Pennington et al., 2004; Higgins, 2017; Mucina, 2019) and the evolutionary processes that interact with filters and species relations (HilleRisLambers et al., 2012; Cavender-Bares et al., 2016). Here, Pinto-Ledezma et al. use a phylo-functional approach to partition beta diversity into two major sources of community compositional change: nestedness, representing change attributed to species loss; and turnover, arising from species replacement. The analysis spans the biomes of North America, and reveals that diversity in species-rich biomes with stable environments tends to arise from a combination of speciation processes and local environmental sorting. Together these produce species turnover along environmental gradients. Differences in biogeographic histories predict patterns of functional similarity among and within these biomes, with nestedness being more important for functional change than turnover.

Biome history is viewed through a different lens by Fox et al. who examine the geologic history of tropical grassy biomes. These biomes were assembled via the increasing abundance of grasses using the C_4 photosynthetic pathway, which came to dominate open, tropical habitats during the late Miocene (Osborne and Beerling, 2006; Edwards et al., 2010; Strömberg, 2011). This biome assembly caused major shifts to present-day tropical carbon cycling (Still et al., 2003) as well as past and present fire regimes (Scheiter et al., 2012). Yet the climate responses of disjunct savanna ecosystems differs considerably across continents (Lehmann et al., 2014). Fox et al. analyze more than 2,600 fossil isotope values to document global Neogene variation in C_4 grass abundance. They find significant but fairly weak agreement between isotope proxy values and climate-driven model predictions of varying complexity. This suggests historic roles for disturbance, biogeographic history, and local ecology in influencing patterns of ecosystem change and function, matching the situation in modern grassy ecosystems (Griffith et al., 2015). These factors are neither fully incorporated into current ecosystem models nor well represented in biome classifications.

The way in which biomes are classified has major impacts for conservation, landscape management, and projected ecosystem change (Pennington et al., 2004; Banda et al., 2016; Lehmann and Parr, 2016; Moncrieff et al., 2016; Griffith et al., 2017). Savannas are often misclassified as degraded forests, resulting in mismanagement of fire regimes and tree planting in ancient grassy ecosystems. Tropical and subtropical savannas are distinguishable from forests by a flammable C_4 grass understory and trees adapted to fire, despite overlap in tree cover values (Scholes and Archer, 1997; Ratnam et al., 2011). Here, Solofondranohatra et al. use grass phylogeny, vegetation surveys, and trait data to extend this concept to differentiate the evolutionary history and function of the understory. They provide new evidence to show that woodland regions of Madagascar are phylogenetically and functionally savannas and not degraded forests, as is asserted by many current biome classifications. In southern India, Ratnam et al. examined a range of vegetation types and found that much of the vegetation previously classified as forests was functionally savannas, having tree species with traits associated with frequent fires. This suggests that current fire suppression practices may be inappropriate for large areas of this region. Conversely, Dexter et al. show that dry forests in South America are functionally distinct from both savannas and moist forests. Dry forests are characterized by tree species adapted to seasonal drought stress and high soil fertility, but lack fire as a significant ecological driver. This means that conservation of dry forest ecosystems also requires unique management practices. Furthermore, these functional differences have a major influence on the nature of biome boundaries and transitions among biome states. For example, Dexter et al. suggest that transition zones between dry and moist forests may be dominated by changes in water availability, whereas transitions between savannas and moist forests may be sharp boundaries characterized by feedbacks and alternative stable states (Hoffmann et al., 2012).

Phylo-functional variation within biomes likely influences the response of ecosystems to climate change and helps explain different functioning among the same biome type on different continents (Lehmann et al., 2014). A major source of variation in savannas across continents is the species pool of trees from which fire-tolerant savanna trees evolved. Stevens et al. provide evidence from a continental-scale transplant experiment that the range of two dominant African savanna trees is most limited by their ability to escape the fire trap. This work further highlights that models of species distributions in savannas, and models of savanna ecosystems in general, will be inappropriate when only considering climatic descriptors of species ranges. Intraspecific trait variation is another source of functional differentiation within biomes. Bachle et al. assembled available data for key functional traits of *Andropogon gerardii*, a dominant grass species of the US Great Plains. Their synthesis suggests that this grass's high abundance and widespread distribution is enabled by its functional attributes and the potential for intraspecific variation to buffer populations against climatic variation. This finding echoes the general finding of Echeverría-Londoño et al. that widespread species will be less specialized functionally. Furthermore, Bachle et al. expose a surprising dearth of functional data for *A. gerardii*, especially given that they focus one of the most well-studied grasses and ecosystems in the world. This reinforces the observation from data syntheses (e.g., Echeverría-Londoño et al.; Pinto-Ledezma et al.), and in fact all studies in this special issue, that vastly more phylogenetic and functional data are required to appropriately understand and project biome function and distribution into the future.

This special issue highlights that, across multiple levels of biological organization, biomes still provide an important conceptual framing of global ecology. Biome classifications are most successful when they include functional and phylogenetic information, and when they allow biomes and boundaries to emerge from species-level data and ecological interactions, rather than imposed by PFT associations with climate and soils. Functional biome classification and mapping approaches will better encapsulate the evolutionary history that produced modern ecosystem function. These studies outline a massive challenge for ecologists and modelers in order to help predict and mitigate rapid and potentially irreversible modifications to the functioning of Earth's biomes.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

FUNDING

This work was supported by NSF award 1342703 (CS and DG).

ACKNOWLEDGMENTS

Thank you to the contributing authors for making this special issue successful. Thank you to the Frontiers in Ecology and Evolution editorial staff and reviewers for their assistance.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.