





Global mismatches in aboveground and belowground biodiversity

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Abstract: *Human activities are accelerating global biodiversity change and have resulted in severely threatened ecosystem services. A large proportion of terrestrial biodiversity is harbored by soil, but soil biodiversity has been omitted from many global biodiversity assessments and conservation actions, and understanding of global patterns of soil biodiversity remains limited. In particular, the extent to which hotspots and coldspots of aboveground and soil biodiversity overlap is not clear. We examined global patterns of these overlaps by mapping indices of aboveground (mammals, birds, amphibians, vascular plants) and soil (bacteria, fungi, macrofauna) biodiversity that we created using previously published data on species richness. Areas of mismatch between aboveground and soil biodiversity covered 27% of Earth's terrestrial surface. The temperate broadleaf and mixed forests biome had the highest proportion of grid cells with high aboveground biodiversity*

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but low soil biodiversity, whereas the boreal and tundra biomes had intermediate soil biodiversity but low aboveground biodiversity. While more data on soil biodiversity are needed, both to cover geographic gaps and to include additional taxa, our results suggest that protecting aboveground biodiversity may not sufficiently reduce threats to soil biodiversity. Given the functional importance of soil biodiversity and the role of soils in human well-being, soil biodiversity should be considered further in policy agendas and conservation actions by adapting management practices to sustain soil biodiversity and considering soil biodiversity when designing protected areas.

Keywords: aboveground-belowground, bacteria, fungi, global patterns, macrofauna, mismatch, policy, soil biodiversity

Disparidades Mundiales entre la Biodiversidad Sobre y Bajo el Suelo

Resumen: Las actividades humanas están acelerando el cambio en la biodiversidad mundial y han tenido como resultado unos servicios ambientales severamente amenazados. Una gran proporción de la biodiversidad terrestre está albergada en el suelo, pero la biodiversidad de este ha sido omitida de varias evaluaciones mundiales de biodiversidad y de las acciones de conservación, además de que el entendimiento de los patrones mundiales de la biodiversidad del suelo permanece limitado; particularmente, la extensión del traslape entre los puntos fríos y calientes de biodiversidad sobre y bajo suelo no está clara. Examinamos los patrones mundiales de estos traslapes mapeando los índices de biodiversidad sobre el suelo (mamíferos, aves, anfibios y plantas vasculares) y bajo el suelo (bacterias, hongos y macrofauna) que creamos con datos previamente publicados de la riqueza de especies. Las áreas de disparidad entre la biodiversidad sobre y bajo el suelo cubrieron el 27% de la superficie terrestre del planeta. El bioma de los bosques templados de plantas frondosas y mixtas tuvo la proporción más alta de celdas de cuadrícula con una biodiversidad alta sobre el suelo, pero baja para en el subsuelo, mientras que los biomas boreales y de la tundra tuvieron una biodiversidad intermedia bajo el suelo, pero baja para el sobre suelo. Aunque se requieren más datos sobre la biodiversidad del suelo, tanto para cubrir los vacíos geográficos como para incluir a taxones adicionales, nuestros resultados sugieren que la protección a la biodiversidad sobre el suelo puede no reducir suficientemente las amenazas para la biodiversidad del suelo. Dada la importancia funcional de la biodiversidad del suelo y el papel de los suelos en el bienestar humano, se debería considerar a la biodiversidad del suelo mucho más en las agendas políticas y en las acciones de conservación, adaptando a las prácticas de manejo para que mantengan a la biodiversidad del suelo y la consideren cuando designen áreas protegidas.

Palabras Clave: bacterias, biodiversidad del suelo, disparidad, hongos, macrofauna, patrones mundiales, políticas, sobre suelo - bajo suelo

摘要: 人类活动正在导致全球生物多样性的快速变化, 并已严重影响到生态系统服务功能。陆地生物多样性中很大一部分存在于土壤之中, 然而, 许多全球生物多样性评估和保护行动都没有考虑土壤生物多样性, 人们对全球土壤生物多样性格局的认识也十分有限, 特别是对地表生物多样性和土壤生物多样性的热点地区及贫瘠地区的重叠程度知之甚少。为了研究全球地表生物多样性和土壤生物多样性的重叠情况, 我们利用已发表的物种丰富度数据设计了地表生物多样性(哺乳动物、鸟类、两栖类、维管植物)及土壤生物多样性(细菌、真菌、大型动物群)指标, 用于绘制相应的地图。结果显示, 地表和土壤生物多样性不匹配的地区占地球陆地面积的 27%。在温带阔叶林和混交林生物群中, 地表生物多样性高而土壤生物多样性低的栅格占比最高, 而寒带和苔原生物群则是土壤生物多样性中等而地表生物多样性低。虽然还有待增加土壤生物多样性的数据以囊括更多地理区域和生物类群, 但我们的结果已经表明, 保护地表生物多样性可能不足以减少对土壤生物多样性的威胁。鉴于土壤生物多样性的重要功能以及土壤对人类福祉的作用, 应在政策议程和保护行动中更多地考虑土壤生物多样性, 如调整管理实践以保护土壤生物多样性、在保护区设计中纳入土壤生物多样性等等。【翻译: 胡怡思; 审校: 聂永刚】

关键词: 地表-地下; 细菌; 真菌; 全球格局; 大型动物群; 不匹配; 政策; 土壤生物多样性

Introduction

The ability of humans to address some of the key challenges of the times, such as a lack of food security and water purification, depends in part on human interactions with soil. Soils are essential for maintaining a wide range of highly important ecosystem services, such as

nutrient cycling, carbon storage, and medical resources (Wall et al. 2013; Bardgett & van der Putten 2014). Yet soil biodiversity faces dramatic declines due to human activities, particularly land-use change and agricultural intensification (Tsiafouli et al. 2015). This is alarming given the substantial global gaps in knowledge of soil biodiversity (Phillips et al. 2017; Cameron et al. 2018),

which have likely been a major factor limiting attempts to address declines in soil biodiversity with policy at large scales. Since the release of the first global report on soil biodiversity (Orgiazzi et al. 2016), data availability has been improving.

Building on this, as well as existing knowledge of aboveground biodiversity, we examined whether the typical focus on conserving aboveground taxa also serves the purpose of protecting the functionally important but less visible soil biodiversity. Previous research suggests hotspots of aboveground (Myers et al. 2000) and soil biodiversity may not correspond because different factors (e.g., soil pH) act as key drivers of biogeographical patterns belowground (Fierer & Jackson 2006; Parker 2010). To this end, we compared commonly used vertebrate and plant data sets with recent global data sets on soil taxa (macrofauna, fungi, and bacteria). We also devised recommendations for incorporating soil biodiversity into conservation planning and global policy targets.

Methods

We created a global map of the overlap between aboveground and soil biodiversity (Fig. 1; detailed methods in Supporting Information). An aboveground biodiversity index was created by combining global data sets of aboveground species richness of vertebrates (mammals, birds, and amphibians) (BirdLife International, NatureServe 2011; IUCN 2012) and vascular plants (Kreft & Jetz 2007). While plants are not strictly aboveground organisms, we considered them as such because plant diversity was assessed aboveground.

A soil biodiversity index was similarly created by harmonizing species richness data from 3 of the largest global data sets available on soil biodiversity—soil macrofauna (Mathieu & Lavelle 2016) ($n = 2163$ sites), fungi (Tedersoo et al. 2014) ($n = 365$ sites), and bacteria (Bahram et al. 2018) ($n = 197$ sites). Soil macrofauna groups included earthworms, ants, termites, spiders, millipedes, centipedes, isopods, fly larvae, cockroaches and mantids, moth and butterfly larvae, grasshoppers and crickets, gastropods, beetles, and other macrofauna (Mathieu & Lavelle 2016). Fungal and bacterial data sets were based on metabarcoding the ITS2 and 16S regions, respectively (Tedersoo et al. 2014; Bahram et al. 2018). These 3 groups represent an important subset of all soil organisms but do not include all groups of soil biota. Additional global data sets on soil bacteria are now being published (Delgado-Baquerizo et al. 2018; Ramirez et al. 2018), and data sets on other soil taxa are currently being compiled, which should be incorporated into more detailed future analyses of mismatches of aboveground and soil biodiversity.

Results

Areas of mismatch between aboveground and soil biodiversity covered 27% of the terrestrial surface of Earth. Regions where aboveground biodiversity was high but soil biodiversity was low were in parts of Colombia, Brazil, Portugal, Spain, Eastern Europe, west-central Africa, Malaysia, Indonesia, Papua New Guinea, and the Midwestern United States (Fig. 1). Temperate broadleaf and mixed forests had the highest proportion of grid cells with high aboveground biodiversity but low soil biodiversity (Supporting Information). The opposite pattern occurred of intermediate to high soil biodiversity but low aboveground biodiversity in parts of India, northern China, and northern Australia (Fig. 1). Soil biodiversity was at an intermediate level but aboveground biodiversity was low in a large portion of the globe's northern regions, such as the boreal and tundra regions of Canada and Russia. Aboveground biodiversity continued to decrease toward the North Pole even at high latitudes, but soil biodiversity reached a plateau (e.g., Tedersoo et al. 2014; Bahram et al. 2018).

Only 37% of the areas with the highest (top 25%) aboveground or soil biodiversity overlapped. Thus, if only areas with the highest aboveground biodiversity are conserved, more than half of the areas with the greatest soil biodiversity are at risk of degradation. Nonetheless, joint hotspot and coldspot areas occurred across 73% of terrestrial ecosystems. Joint hotspots occurred in the equatorial regions of South America, Central America, Central Africa, and parts of Southeast Asia, and in particular in the tropical and subtropical moist broadleaf forests biome (Fig. 1 & Supporting Information). In contrast, joint coldspots mostly occurred in deserts (e.g., the Sahara), as well as in parts of the boreal forest-taiga biome.

Standard deviation around the mean biodiversity values was higher for soil biodiversity than aboveground biodiversity (Supporting Information). Standard deviation values for soil biodiversity were highest in parts of the Amazon, central Africa, central Asia, Malaysia, and Indonesia, which are some of the regions where soil biodiversity data are particularly lacking. Most of the patterns of matches and mismatches for subsets of taxa (Supporting Information) were similar to the patterns for all aboveground and all soil biodiversity. For example, when soil macrofauna and aboveground biodiversity were mapped (i.e., soil microbes were not included), the only substantial difference was that part of west-central Africa became a joint soil and aboveground biodiversity hotspot, rather than having high aboveground biodiversity but low soil biodiversity. Mapping soil microbial biodiversity in relation to aboveground biodiversity resulted in larger differences. In particular, areas that were joint hotspots in South America, central Africa, and Madagascar when both soil macrofauna and microbial data were mapped together became aboveground biodiversity hotspots with

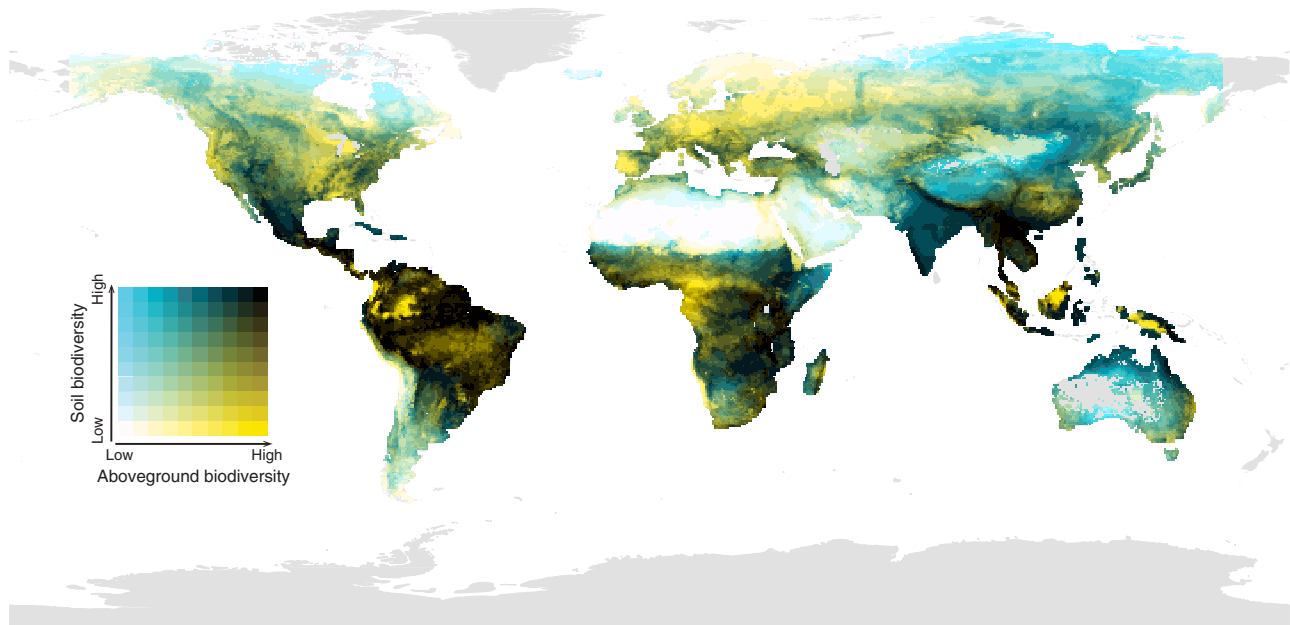


Figure 1. Global distribution of the overlap between aboveground (mammals, birds, amphibians, plants) and soil (macrofauna, fungi, bacteria) biodiversity (dark areas, high aboveground and soil biodiversity; bright yellow, high aboveground but low soil biodiversity; bright blue, low aboveground but high soil biodiversity; white, low aboveground and soil biodiversity; gray, insufficient data). The color scale is based on quantile intervals with each class containing an equal number of biodiversity features.

low soil biodiversity when only soil microbial biodiversity was mapped. Overlap of plant biodiversity and soil biodiversity and vertebrate biodiversity and soil biodiversity were highly similar to overlap of aboveground and soil biodiversity (Fig. 1).

Discussion

The mismatches we found suggest that conserving aboveground biodiversity will not be sufficient to protect soil biodiversity, and thus policy changes and conservation actions must be taken to manage key threats. Understanding of global patterns is restricted by substantial soil biodiversity data gaps in key regions such as Africa and Russia, in particular central Africa and Siberia (Bahram et al. 2018; Cameron et al. 2018), as well as a lack of global data sets on taxa such as microarthropods and nematodes. The lack of data on microbes aboveground (e.g., on leaves) and parasites in general, which are also not typically considered in conservation efforts, is another major gap in understanding.

An additional limitation of our analysis is that the data sets we used differed in taxonomic resolution (e.g., the macrofauna data set included data on groups of macrofauna, such as earthworms, rather than data at the species level or operational taxonomic unit level), which may make comparisons difficult. Also, molecular methods were used to obtain microbial data (which may

contain DNA of organisms that are no longer living), whereas classic taxonomic methods were used for the other taxa (which mostly cover active organisms and not resting stages, for example). In fact, the analysis where soil microbial biodiversity was overlain in relation to aboveground biodiversity (Supporting Information) differed more substantially from the all-taxa analysis (Fig. 1) than did the other analyses that examined separate groups of taxa (Supporting Information). This issue should be considered in future analyses of aboveground-soil biodiversity mismatches as availability of data improves.

Nonetheless, some general recommendations can be drawn from our analysis, combined with previous research. Intensive human exploitation and soil degradation are critical threats in regions with high soil biodiversity; risks are especially high in agricultural areas (Tsiafouli et al. 2015). For example, soil biodiversity is relatively high in India, especially along the northeast border, which is a joint hotspot for aboveground and soil biodiversity (Fig. 1), but this same region also has one of the highest densities of cropland in the world (Klein Goldewijk et al. 2011). Agricultural intensification affects soil biodiversity across functional groups through a range of management practices, such as application of high levels of pesticides and fertilizers as well as intensive tillage (FAO & ITPS 2015; Tsiafouli et al. 2015). To minimize impacts, reduced-till and no-till systems should be implemented where possible, pesticide and fertilizer

applications should be reduced, and reclamation of degraded land should be increased.

Threats to soil biodiversity should also be managed by considering soil biodiversity in protected areas planning and conservation prioritization (Parker 2010; Orghiazzi et al. 2016). This is likely to be most feasible in regions where relatively high soil biodiversity coincides with low human population densities but that are also threatened by future resource extraction. Specifically, to protect soil biodiversity hotspots while minimizing conflicts with human land use, designation of new or expansion of existing protected areas in boreal and tundra regions (where soil biodiversity is intermediate and aboveground biodiversity is low [Fig. 1]) should be a top priority, given the pronounced climate change expected (IPCC 2013) and the functional importance for carbon storage of those regions (Tarnocai et al. 2009). These regions have soil high in organic matter in contrast to the thinner organic soil layer found in tropical forests, which may help support high soil biodiversity but not necessarily aboveground biodiversity. Furthermore, these rich organic soils are critical for global carbon dynamics, and soil biodiversity contributes to these dynamics. Any measures to conserve soil (as well as aboveground) biodiversity hotspots worldwide will be compromised without corresponding action to address climate change, and major national and international efforts focused on managing both land use and climate change are required.

The compelling evidence of the strong links between soil biodiversity and provisioning of ecosystem services (Wall 2004; Wall et al. 2013) needs to be better translated into policies. For example, soil biodiversity should be incorporated more explicitly in global initiatives, such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and the 2020+/2030 strategy of the Convention on Biological Diversity. As well, the UN Convention to Combat Desertification recently endorsed the Scientific Conceptual Framework for Land Degradation Neutrality, which calls for no decrease in the amount and quality of land resources within specified temporal and spatial scales (Orr et al. 2017). Reclamation to restore degraded lands, as called for in this framework, benefits both soil biodiversity and ecosystem functioning.

In addition to participating in global assessments, further work is needed to collect data on soil biodiversity patterns, such as endemism, and to determine how knowledge on the relationship between soil biodiversity and ecosystem functioning can be scaled up from plot level to a global scale. The critical next step will be to use these large-scale data sets, developed through synthesis or assessments, to determine what to conserve to maintain vital ecosystem services. Cooperation with policy makers and conservation scientists is essential for this to be successful.

In conclusion, the neglect of soil biodiversity in policy agendas and conservation debates thus far is decreasing and can be further corrected in the future by filling data gaps in knowledge of global distributions of soil taxa to allow improved mapping; adapting management practices to sustain soil biodiversity in the long term (e.g., in relation to agriculture [Tsiafouli et al. 2015]); considering soil biodiversity when designing or enlarging protected areas (e.g., in boreal and tundra regions); and incorporating knowledge of soil biodiversity into local to global policies and biodiversity and ecosystem services assessments.

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Supporting Information

Detailed methods (Appendix S1), maps showing the means and standard deviations of aboveground and soil biodiversity indices (Fig. S1; Appendix S2), maps showing the overlap between subsets of aboveground and soil taxa (Fig. S2; Appendix S2), and matches and mismatches in different biomes (Table S1; Appendix S2), are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Supporting Information

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