UN-REDD
PROGRAMME

Carbon and biodiversity relationships in tropical forests

UN-REDD Programme

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Multiple Benefits Series **4**

The UN-REDD Programme, a collaborative partnership between FAO, UNDP and UNEP, was created in response to, and in support of, the UNFCCC decision on REDD at COP 13 and the Bali Action Plan. The Programme supports countries to develop capacity to reduce emissions from deforestation and forest degradation and to implement a future REDD mechanism in a post-2012 climate regime. It builds on the convening power of its participating UN agencies, their diverse expertise and vast networks, and "delivers as One UN".

The United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) is the biodiversity assessment and policy implementation arm of the United Nations Environment Programme (UNEP), the world's foremost intergovernmental environmental organization. The centre has been in operation since 1989, combining scientific research with practical policy advice.

The United Nations has proclaimed 2010 to be the International Year of Biodiversity. People all over the world are working to safeguard this irreplaceable natural wealth and reduce biodiversity loss. This is vital for current and future human wellbeing. We need to do more. Now is the time to act.

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Summary

This paper provides an overview of the current state of knowledge regarding relationships between carbon and biodiversity in tropical forests.

- At a global scale, tropical forests provide some of the highest levels of biomass carbon storage, productivity and biodiversity.
- Within tropical forests, spatial patterns of carbon dynamics and biodiversity are complex, with limited correlations between these variables.
- There are a number of environmental and historical factors that may have caused the observed variations in carbon dynamics and biodiversity across the tropics.
- The degree to which direct causal relationships exist between carbon dynamics and biodiversity in tropical forests is still uncertain, although experimental work in other ecosystems has shown that biodiversity often promotes productivity and stability.
- Areas of ongoing uncertainty include: the temporal variability of ecosystem processes and their response to environmental change; the importance of interactions between species, and the quantification of carbon stocks and fluxes in tropical soils and below-ground biomass

Relations entre le carbone et la biodiversité dans les forêts tropicales : Résumé

Ce dossier donne une vue d'ensemble de l'état actuel des connaissances sur les relations entre le carbone et la biodiversité dans les forêts tropicales.

- À l'échelle globale, les forêts tropicales fournissent les taux les plus élevés de stockage de carbone, de productivité et de biodiversité.
- Dans les forêts tropicales, les répartitions spatiales des dynamiques du carbone et de la biodiversité sont complexes, avec des corrélations limitées entre ces deux variables.
- Il y a un nombre de facteurs environnementaux et historiques qui ont peut-être contribués aux variations observées sur les dynamiques du carbone et la biodiversité à travers les tropiques.
- La mesure dans laquelle il existe un lien de causalité direct entre les dynamiques du carbone et la biodiversité dans les forêts tropicales n'est pas certaine, bien que des travaux expérimentaux dans d'autres écosystèmes aient démontrés que la biodiversité promeuve souvent la productivité et la stabilité d'un écosystème.
- Des points d'incertitude comprennent : la variabilité temporelle des processus écosystémiques et leurs réactions aux changements environnementaux ; l'importance des

interactions entre espèces ; et la quantification des stocks de carbone et des flux dans les sols tropicaux et dans la biomasse souterraine.

Relaciones entre el carbono y la biodiversidad en los bosques tropicales : Resumen

Este artículo proporciona una visión general del estado actual del conocimiento sobre las relaciones entre el carbono y la biodiversidad en los bosques tropicales.

- A escala global, los bosques tropicales aportan uno de los niveles más altos de almacenamiento de carbono, productividad y biodiversidad.
- En los bosques tropicales, los patrones espaciales de las dinámicas de carbono y de la biodiversidad son complejos, con limitadas correlaciones entre estas variables.
- Existen varios factores ambientales e históricos que pueden haber causado las variaciones observadas en las dinámicas del carbono y la biodiversidad en los trópicos.
- El grado de relaciones causales directas entre las dinámicas del carbono y la biodiversidad en bosques tropicales es aún incierto, aunque trabajos experimentales en otros ecosistemas han mostrado que la biodiversidad a menudo promueve productividad y estabilidad.
- Las áreas de incertidumbre comprenden: la variabilidad temporal de los procesos ecosistémicos y su respuesta al cambio ambiental; la importancia de interacciones entre especies; y la cuantificación de almacenes y flujos de carbono en suelos tropicales y en la biomasa subterránea.

Hubungan antara karbon dan keanekaragaman hayati di hutan-hutan tropis : Ringkasan

Paper ini memberikan tinjauan umum tentang pandangan yang berkembang saat ini sehubungan dengan keterkaitan antara karbon dan keanekaragaman hayati di kawasan hutan tropis.

- Pada skala global, hutan tropis menyediakan sejumlah cadangan karbon biomasa, produktifitas dan keanekaragaman hayati pada tingkat yang sangat tinggi.
- Di dalam hutan tropis, dinamika karbon dan keanekaragaman hayati memiliki pola-pola spasial yang kompleks, dengan korelasi yang terbatas diantara variable-variabel tersebut.
- Terdapat sejumlah faktor historis dan lingkungan yang mungkin telah menyebabkan munculnya variasi-variasi yang teramati pada dinamika karbon dan keanekaragaman hayati di kawasan tropis.

- Masih belum dapat dipastikan sampai sejauh mana terdapat hubungan kausal langsung antara dinamika karbon dan keanekaragaman hayati di hutan tropis, namun upaya percobaan di ekosistem-ekosistem lain telah menunjukkan bahwa keanekaragaman hayati seringkali mampu meningkatkan produktifitas dan stabilitas.

- Hal-hal yang masih mengandung unsur ketidakpastian tersebut adalah: variabilitas temporal dari proses- proses ekosistem dan responnya terhadap perubahan lingkungan; pentingnya interaksi diantara spesies, dan kuantifikasi cadangan karbon serta flux karbon di lahan tropis dan biomasa bawah tanah (*below-ground biomass*).

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1 Introduction

This paper provides an overview of the current state of knowledge regarding relationships between carbon and biodiversity in tropical forests. It considers the extent to which correlations exist between the spatial distributions of carbon and biodiversity, and the possible causal factors affecting these distributions. Gaps in current understanding are also highlighted.

Tropical forests are globally significant for both their biodiversity and their role in the carbon cycle. Maintaining carbon storage within tropical forests is the main objective of the UN Programme for Reducing Emissions from Deforestation and Forest Degradation in developing countries (UN-REDD). Conservation of biodiversity can also be achieved through the implementation of the UN-REDD Programme, but this outcome is not guaranteed. It requires an understanding of how carbon dynamics and biodiversity interact. This will better allow forests with high diversity to be prioritised for REDD schemes and improve awareness of forests not covered by REDD, which may require extra protection from conversion pressures.

2 Defining and measuring tropical carbon dynamics and biodiversity

Carbon cycling in tropical forests involves the uptake of carbon from the atmosphere into vegetation during photosynthesis. Any carbon not released through respiration is then stored as biomass, before it is released once more as a result of mortality or other processes. The most commonly measured elements of this cycle are above-ground net primary productivity (ANPP) and above-ground biomass (AGB), although estimates of these variables are often limited to trees, excluding herbs, lianas and epiphytes.

Biodiversity is a broad, multifaceted term that encompasses a wide range of definitions. It may be described through species range maps, rapid inventories, or more intensive surveys concentrating on particular species groups. A common approach in tropical forests is to establish a network of inventory plots, which offer a standardised source of data, repeatable over a long time series and a wide spatial area. In these plots, it is common practice to record only the species diversity of trees above a certain diameter threshold, typically 100mm diameter at breast height.

Species diversity and its spatial variation are commonly described in two ways: *α-diversity* relates to diversity within a plot, while *β-diversity* records differences in species composition between plots, within a wider area. Both α-diversity and β-diversity vary between forests, however β-diversity is strongly affected by the degree of variability of environmental factors, including topography, geology, soils and climate. This between-site variability does not appear to be an important driver of forest carbon dynamics. Variation in α-diversity is more likely to interact with variation in forest carbon dynamics.

3 Spatial distributions of carbon and biodiversity in tropical forests

A global map of carbon storage, biodiversity and conservation priority has shown strong correlations between total biomass and species richness of mammals, birds and amphibians (Figure 1) (Strassburg et al. i2010). Tropical forests score highly on both counts, but biomass, productivity and biodiversity can vary significantly within and between tropical forests. The spatial distribution of these variables can be viewed on a range of scales, from global patterns to local landscapes. Globally, although the highest levels of biodiversity and ANPP are found in tropical forests, the highest AGB is in temperate forests such as those of northern California (Keeling and Phillips 2007).

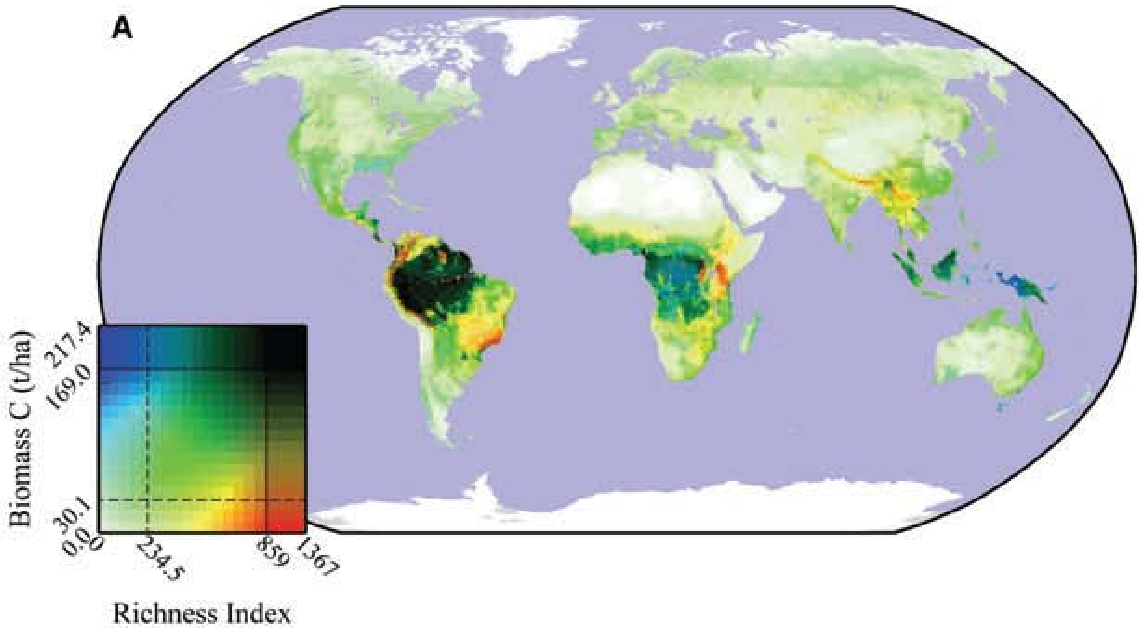
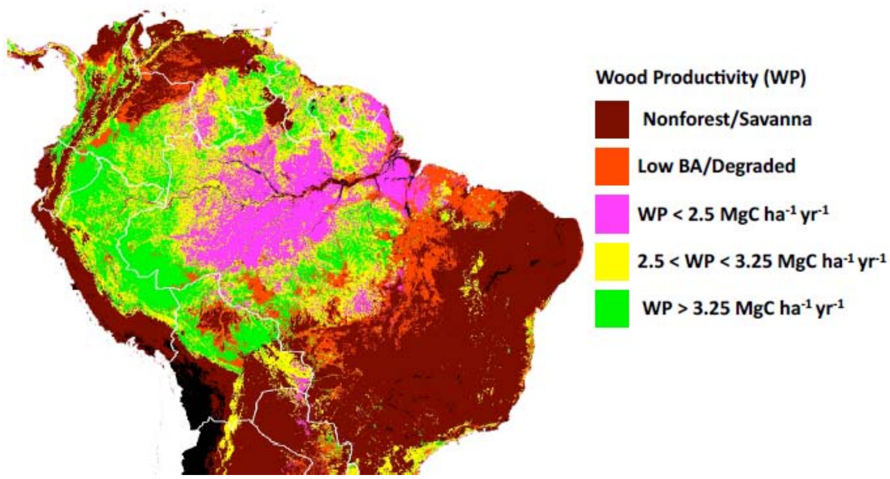


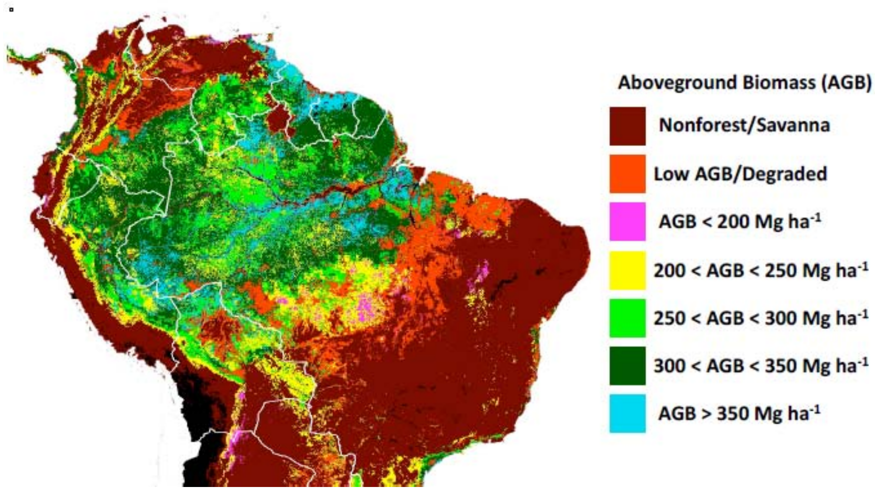
Figure 1: Global congruence between biomass carbon and overall species richness of mammals, birds and amphibians. The two-dimensional colour scale used displays both the concentration of biomass carbon and biodiversity and the congruence. From Strassburg et al. (2010).

On a continental scale, tropical AGB is highest in the Dipterocarpaceae forests of SE Asia (Chave et al. 2008; Laumonier et al. in press; Paoli et al. 2008), and lower in Africa (Lewis et al. 2009b) and South America (Baker et al. 2004). Biodiversity reveals a different pattern, with lower floristic diversity in African forests than in the other tropical continents. Mean α-diversity levels in African tropical forests, at least in terms of tree species, are only half of those in South America (Parmentier et al. 2007). Asian forests have similar mean α-diversity to South American forests.

Within Amazonia, above-ground coarse woody productivity (WP, closely related to ANPP) varies between 1.5 and 5.5 Mg C ha^{-1} a^{-1} (Malhi et al. 2004). The most productive forests, with WP above 3.25 Mg C ha^{-1} yr^{-1}, are found in western Amazonia and the Andean foothills (Figure 2), in a zone stretching from Colombia, through Ecuador and Peru to Bolivia (Saatchi et al. 2009). The Amazonian forests which the highest α-diversity can be found in a latitudinal band running across the centre of the tropical forest zone at 5°S, with high values concentrating especially in the western part of this band (Figure 3). Forests with the lowest α-diversity are found at the extreme northern and southern fringes of the tropical forest zone, in the Guyana Shield and Bolivia (ter Steege et al. 2003).



(a)



(b)

Figure 2: Distributions of (a) above-ground coarse wood productivity and (b) aboveground biomass from classification of Maxent model predictions using 135 and 226 forest plots respectively, plus environmental variables. From Saatchi et al. (2009).

There is thus some correlation between the spatial distributions of productivity (as measured by WP) and tree species diversity in Amazonia, since both peak in the west, around northern Peru and Amazonian Ecuador. However, productivity is also high in Bolivia, which has relatively low diversity, and diversity is high in Central Amazonia, which has relatively low productivity. Biomass and biodiversity appear to show little correlation in Amazonia (Figures 2 and 3). AGB peaks in eastern Amazonian and the Guiana Shield, where diversity is low. However, both AGB and α-diversity record their lowest values in the southern and northern fringes of Amazonia (Saatchi et al. 2009).

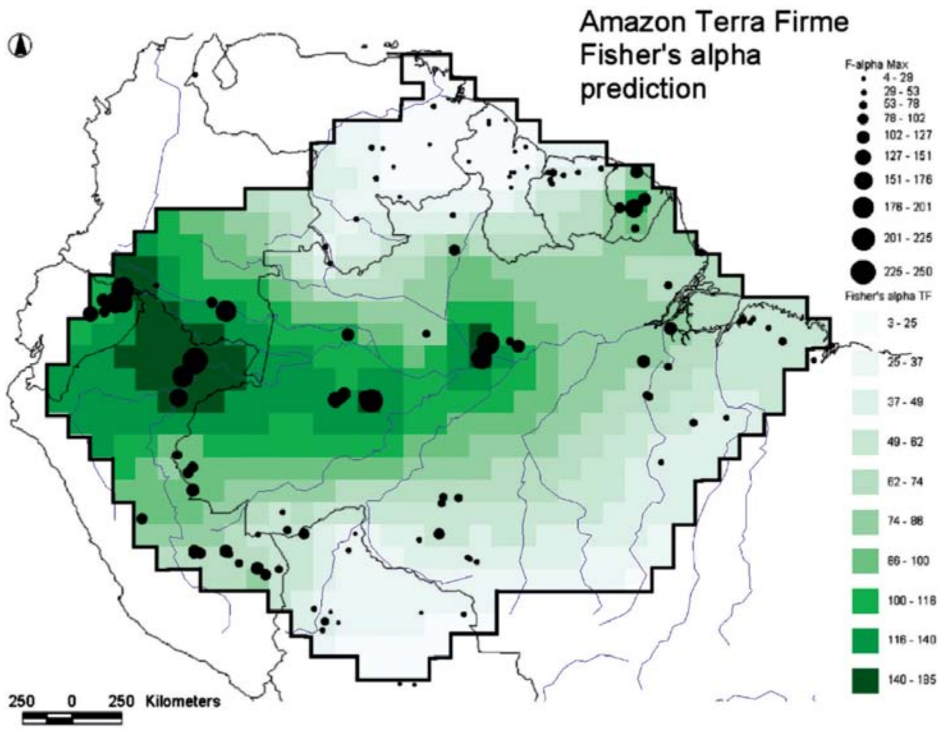


Figure 3: Map of average tree α-diversity (Fisher's α) based on 275 plots in terra firme forest in the Amazon and Guayana Shield rain forest area mapped on a 1° grid cell scale. Dots indicate the maximum Fisher's α found at one location (n = 275; fewer than 275 dots are visible because many plots are in close proximity (and in some case overlapping). From ter Steege et al. (2003).

In African forests, AGB is highest in the western Congo Basin. The Central and Eastern Congo Basin have intermediate levels of AGB, while the lowest AGB is found in West Africa and the fringes of the tropical forest area (Baccini et al. 2008). Tree α-diversity is also lower in West Africa than in Central Africa (Parmentier et al. 2007).

4 Causes of variation in forest carbon dynamics and biodiversity

The existence of correlations between the spatial distributions of biomass, productivity and biodiversity does not necessarily indicate a direct causal link between these variables. Analysis is complicated by a wide range of co-varying environmental factors, such as present and past climates, geology, soil characteristics, topography, disturbance regimes, and evolutionary and geological history. A combination of these factors may give rise to the observed spatial distributions, through their effects on carbon dynamics, or biodiversity, or both. It is likely that these distributions are the result of a complex network of interactions, involving a large numbers of variables.

There is no simple correlation between productivity and biomass, as higher productivity does not always result in higher biomass. There is some evidence that AGB actually declines when ANPP reaches the highest levels found in tropical forests. This is because high productivity causes high turnover rates, and these promote fast-growing species with low wood density (Keeling and Phillips 2007). High turnover rates are also associated with high mortality, high disturbance levels in terms of treefall gaps, and reduced longevity of individual trees. Low wood density and reduced individual longevity are two key determinants of lower AGB.

The most important driver of regional variability in productivity across Amazonia appears to be soil fertility. Quesada et al. (2009) found that soil fertility, especially available soil phosphorus, has a strong positive effect on the coarse wood production of Amazonian forests, leading to the spatial pattern described above. Meanwhile, tree turnover rates were found to be more strongly controlled by soil physical properties. Regional variation in AGB is mainly determined by variation in mean wood density (Baker et al. 2004), which is related to species composition, and is negatively correlated with productivity, as described above.

There has been extensive research into the origins and maintenance of the exceptionally high biodiversity found in tropical forests; however these mechanisms are still not fully understood. Species-area theory suggests the diversity of a biome is dependent on a combination of its area and the amount of time it has existed (Fine and Ree 2006). Accordingly, diversity is highest in the latitudinal band that cuts through the centre of Amazonia because this is the centre of the tropical forest zone, and because it has experienced the most stable climate.

It has been proposed that the warm, moist tropical climate promotes faster speciation rates, allows denser niche packing, and maximises the number of species that can tolerate the prevailing environmental conditions (Currie et al. 2004). Past climates are also important in determining diversity, since speciation is a slow process. Past reductions in the extent of the African tropical moist forest zone (during glaciations) could explain the low diversity levels in African forests, especially the low diversity of species adapted to warm, wet conditions, compared to South American forests with equivalent climatic conditions (Parmentier et al. 2007). Many other mechanisms have been proposed to explain high tropical biodiversity, including neutral theory (Hubbell 2001), which considers dispersal limitations to be more important than inter-species differences; and density- or distance-dependent mortality (Wills et al. 2006), which favours the survival of locally rare species over locally common ones.

In addition to the factors described above, it is possible for direct relationships to exist between carbon dynamics and biodiversity. In many ecosystems, research has shown that biodiversity can have a positive impact on productivity in temperate grasslands and other non-forest ecosystems (Cardinale et al. 2007; Tilman et al. 2001). These effects may be due to niche differentiation, which may allow more resources to be tapped when biodiversity is greater.

Applying these ideas to mature tropical forests is problematic, because it is difficult to control for all the other environmental variables that exist within these forests. However, in an experimental study of tree seedlings, planted in monocultures and in mixed-species plots in central Panama (Potvin and Gotelli 2008) mixed-species plots had a mean 30-58% higher total basal area than monocultures after five years due to enhanced productivity (diversity had no apparent effect on mortality rates).

5 Areas requiring further research

Tropical forest ecology has come a long way in recent years, but there are still many areas where the level of knowledge is insufficient. This section highlights some of the relevant gaps in our understanding.

Direct relationships between biodiversity and carbon dynamics in mature tropical forests are poorly understood. The nature of these forests, in particular the exceptionally high diversity and the extremely long lifespan of the trees, makes it impractical to plant experimental plots to represent natural forests. Observational studies are possible, but these must be designed in a way that deals satisfactorily with all of the co-varying environmental variables.

The relatively long time intervals between censuses in most forest inventory plots make it difficult to study the temporal variability of ecological processes. The temporal variability of litterfall (Chave et al. 2009) is better understood than the temporal variability of other processes related to carbon dynamics. Better knowledge is needed about the stability of these processes, and their resilience to disturbance and extreme events. The influence of environmental change also need to be considered and could have major impacts on tropical forest biodiversity (Miles et al. 2004).

The major global networks of tropical forest inventory plots (Chave et al. 2008; Peacock et al. 2009) mostly concentrate on trees above a certain diameter threshold, typically 100mm diameter at breast height. Trees above this threshold typically comprise over 80% of total AGB (Baker et al. 2004), so it makes sense to focus on them. However, it is important not to overlook the role of other taxa. Recent research has explored the interactions between lianas and trees (Schnitzer et al. 2008). Large mammals may have an impact on forest structure and species composition (Brodie and Gibbs 2009), but these impacts have been little studied.

In forest inventory plots, ANPP (WP) and AGB are commonly measured, rather than total net primary production and total biomass, due to the difficulties of accurately estimating below-ground carbon stocks. Therefore, the spatial patterns found may represent spatial variation in the balance of carbon allocation between respiration, wood carbon and fine root production, rather than variability in gross primary productivity (Malhi et al. 2004).

As well as living and dead biomass, the soil is also a major store of carbon, which has not been addressed in most of the studies reviewed here. In particular, tropical peat soils hold up to 70 Pg C (Takashi et al. 2007). These soils are particularly widespread in Indo-Malaya, but can also be found in other tropical regions. Net Ecosystem Productivity (NEP) is a more complete measure than ANPP, since it records the balance of photosynthesis and respiration within the entire ecosystem, including microbial and plant-based soil respiration, and would therefore account for soil carbon changes. NEP across a 50-100ha area can be estimated using flux towers and eddy-covariance techniques, but correction factors have to be applied (Lewis et al. 2009a) to account for CO_2 fluxes on calm nights, which are not otherwise captured.

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