



Co-occurrence of biodiversity, carbon storage, coastal protection, and fish and invertebrate production to inform global mangrove conservation planning

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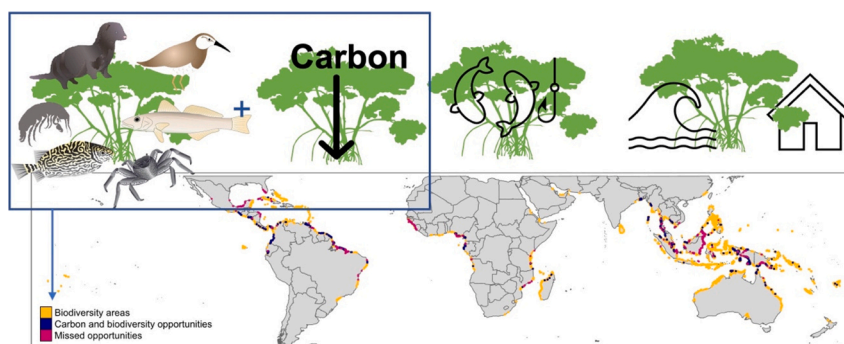
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HIGHLIGHTS

- Conservation planning requires knowledge of what opportunities exist and where.
- We bring together global data on four key mangrove ecosystem services (ES).
- Hotspots of ES and co-occurrence of ES occurred throughout the world.
- Even when ES rarely co-occurred in nations, some sites provide high-value benefits.
- We provide a precursor for decisions about where and how to invest in conservation.

GRAPHICAL ABSTRACT



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ABSTRACT

Mangrove forests support unique biodiversity and provide a suite of ecosystem services (ES) that benefit people. Decades of continual mangrove loss and degradation have necessitated global efforts to protect and restore this important ecosystem. Generating and evaluating asset maps of biodiversity and ES is an important precursor to identifying locations that can deliver conservation outcomes across varying scales, such as maximising the co-occurrence of specific ES. We bring together global datasets on mangrove-affiliated biodiversity, carbon

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Fisheries
Restoration
Spatial-planning
Wildlife

stocks, fish and invertebrate production, and coastal protection to provide insight into potential trade-offs, synergies and opportunities from mangrove conservation. We map opportunities where high ES provision co-occurs with these areas that could be leveraged in conservation planning, and identify potential high-value opportunities for single ES that might otherwise be missed with a biodiversity focus. Hotspots of single ES, co-occurrence of multiple ES, and opportunities to simultaneously leverage biodiversity and ES occurred throughout the world. For example, efforts that focus on conserving or restoring mangroves to store carbon can be targeted to deliver multiple ES benefits. Some nations, such as Vietnam, Oman, Ecuador and China, showed consistent (although not necessarily strong) correlations between ES pairs. A lack of clear or consistent spatial trends elsewhere suggests that some nations will likely benefit more from complementarity-based approaches that focus on multiple sites with high provision of different services. Individual sites within these nations, however, such as Laguna de Terminos in Mexico still provide valuable opportunities to leverage co-benefits. Ensuring that an ES focused approach is complemented by strategic spatial planning is a priority, and our analyses provide a precursor towards decisions about where and how to invest.

1. Introduction

Mangrove forests support unique biodiversity on both land and in the sea, including fishes, birds, mammals, and threatened megafauna (Nagelkerken et al., 2008; Rog et al., 2017; Sievers et al., 2019; zu Ermgassen et al., 2020). Mangrove forests enhance fisheries production by supporting resilient and productive food webs and providing nursery habitats (Hutchison et al., 2014; Carrasquilla-Henao and Juanes, 2017), and help adaptation to, and mitigation of, climate change for example by protecting coastal communities from severe weather events (Marois and Mitsch, 2015; Menéndez et al., 2020), and sequestering carbon (O'Connor et al., 2020; Adame et al., 2021). Despite providing extensive ecosystem services (hereafter ES), mangroves have historically undergone significant global losses in their extent and ecological condition (Hamilton and Casey, 2016; Bryan-Brown et al., 2020; Goldberg et al., 2020), and remain susceptible to human pressures, such as those from conversion for aquaculture, oil palm and rice production, and accelerating climate impacts (Friess et al., 2019; He and Silliman, 2019; Tulloch et al., 2020).

The global net rate of loss has declined in the 21st century (Friess et al., 2020), and it is estimated that 43 % of the current mangrove distribution falls within protected areas (UNEP-WCMC, 2022). However, this percentage might be an overestimate (Dabalà et al., 2022) and the degree to which mangroves within protected areas are safeguarded varies considerably (Friess et al., 2019). Conserving, restoring and sustainably using mangrove ecosystems can help advance progress towards commitments made under international conventions seeking to address the climate and climate crises (Griscom et al., 2017; Griscom et al., 2020) and sustainability including the Kunming-Montreal Global Biodiversity Framework, the United Nations Convention on Climate Change, and the Sustainable Development Goals, including Goal 2 (zero hunger), goal 13 (climate action), goal 14 and goal 15 (biodiversity conservation) (Díaz et al., 2019; Friess et al., 2019). However, in order to be as effective as possible, the conservation and restoration of mangroves requires strategic planning and action (Buelow et al., 2022).

Decision-making for where and how to invest in conservation and restoration requires an understanding of where opportunities are located. Generating maps, such as asset maps of biodiversity or ES (e.g., Soto-Navarro et al., 2020; Allan et al., 2022), is a cornerstone of conservation science and provides a 'screening tool' that, along with additional information, can help inform decision making to deliver conservation outcomes across varying scales (Chaplin-Kramer et al., 2021; Tallis et al., 2021). Studies of terrestrial forests have emphasised the importance of identifying areas with a high co-occurrence of biodiversity in funding schemes focused on climate mitigation (e.g., Strassburg et al., 2010; Kessler et al., 2012; Soto-Navarro et al., 2020). Others have broadened analyses by including additional ES such as those related to water (e.g., Greve et al., 2013; Jung et al., 2021) or marine fisheries production (e.g., Sala et al., 2021). Similarly, analyses of mangrove systems have supported national conservation prioritizations, such as those for Fiji (Atkinson et al., 2016), Bangladesh (Rahman

et al., 2021), and Mexico (Adame et al., 2015), whilst global analysis has shown the clear benefits to humanity of including ES when designing protected areas and prioritising mangrove conservation (Dabalà et al., 2022).

Identification and mapping of ES enables trade-offs and synergies to be evaluated across objectives, potentially resulting in "win-win opportunities" for the ES considered, used to maximise complementarity across objectives when spatial congruence is difficult to achieve (e.g., Beger et al., 2015) and to supplement social, political, economic and ethical considerations (see Wyborn and Evans, 2021; Chaplin-Kramer et al., 2022; Fleischman et al., 2022). Such analyses are important as the conservation and policy world moves towards ambitious area-based targets, such as the '30 × 30 initiative' that proposes protecting 30 % of the world's land area by 2030 (UNEP, 2020).

Asset mapping of mangroves ES globally to date has been completed for carbon storage (Hamilton and Friess, 2018), fish and invertebrate abundance (<https://oceanwealth.org/>), and coastal protection (Menéndez et al., 2020). Here we use the broad term ES to reflect *potential* ES, as opposed to *realised* ES, which is the fraction used by society. We combine these global datasets with data on mangrove-affiliated biodiversity (flora and fauna) to: (1) identify the area needed to theoretically protect all mangrove-affiliated biodiversity (hereafter 'biodiversity areas'); (2) calculate the ES co-benefits that can be delivered by safeguarding this biodiversity; (3) map areas where high ES values co-occur; (4) identify opportunities for single ES protection that may be missed with an exclusively biodiversity-focused strategy, and; (5) quantify national-level correlations between services provision to provide insight into potential opportunities for leveraging ES co-benefits within nations.

2. Material and methods

We first developed a prioritization approach to identify mangrove areas that capture a sufficient proportion of habitat to theoretically protect mangrove-affiliated biodiversity. To evaluate where high ES values co-occur, we first mapped areas that were hotspots for one, two or three ES, and separately mapped the top 10 % of cells that collectively maximised service provision based on a summed ranking approach. Although used widely to describe various concepts, here hotspots are simply the top 10 % of cells with respect to the amount of *potential* ES provision. For the latter, we rank cells across all ES and a summed rank is used to identify the top 10 % of cells. As such, cells that are not hotspots for any of the three ES can still be a hotspot for the summed rank approach, for instance, if the cell was ranked just outside the top 10 % for all three ES. Finally, we analyse correlations between pairs of ES at the national scale, using spearman rank correlation coefficients. For an overview of the datasets used in the analysis, see Table S1.

2.1. Global mangrove grid

The spatial framework of this analysis was a 20 × 20 km grid that

intersected the global mangrove habitat extent v2 (Bunting et al., 2018), and filtered to include only grid cells containing mangroves (9321 cells).

2.2. Biodiversity data

We searched the IUCN Red List database (<https://iucnredlist.org>) for species with assigned mangrove affiliations (IUCN habitat categories 1.7 and 12.7). Only taxonomic groups which have been well-assessed were considered in the analysis to minimise geographic and taxonomic bias. These include all mammals, birds and amphibians, as well as selected groups of reptiles, fish and plants (see Appendix A for more information). This resulted in a pool of 1404 species whose spatial distributions we downloaded from the IUCN database, and used in this analysis (see Table S2 for species list). IUCN spatial distributions are based on the best possible map assessors can make, with the final occurrence polygon(s) showing the distribution limits, and not necessarily the precise areas where a species occurs.

2.3. Carbon data

A global raster of carbon stocks and potential emissions in 2010 (Hamilton and Friess, 2018) was aggregated to a spatial resolution of $\sim 1\text{km}^2$, and the mean of nearest neighbours was calculated from focal statistics using an iterative buffer to gap-fill missing values. Carbon data from Hamilton and Friess (2018) comes from estimates of above ground biomass (AGB) derived from a series latitudinal or bioclimatic linear equations, from estimates of belowground biomass (BGB) calculated from an allometrically derived ratio of mangrove AGB, and from soil organic carbon (SOC) levels estimated based on a predictive model of spatially explicit global mangrove soil carbon stocks. We cropped, masked, and extracted these raster values at each cell. The data was then summarised to calculate the total amount of carbon in each cell (AGB, BGB and 1 m SOC). Due to differences between mangrove distribution of the Bunting et al. (2018) vector (polygon) and the rasterised carbon dataset, 0.4 % of cells required further gap-filling. For each cell with missing data a buffer was applied around its centroid. Buffers were used to iteratively assign the mean of all values within buffer of 20 km intervals (20 km, 40 km, 60 km, etc.), until all missing data cells received a carbon value.

2.4. Fish and invertebrate abundance data

The Nature Conservancy Ocean Wealth mapping portal dataset (<https://oceanwealth.org/>) models mangrove commercial finfish abundance (year of young/year) and/or invertebrate abundance (individuals/year) at a spatial resolution of $\sim 1\text{km}^2$. We cropped, masked and extracted raster values for both datasets within each cell. The data was then summarised to calculate the mean finfish and invertebrate abundance (total 37 species) within each cell, hereafter 'fish production'. For both finfish and invertebrate raster datasets, 5.9 % of cells did not contain data. The majority (90 %) of missing cells occurred along the West African coastline which was data deficient and therefore not modelled in the original dataset. The remaining cells did not contain data due to different underlying mangrove distribution datasets being used, and the same gap-filling approach used for carbon data was applied to these cells.

2.5. Coastal protection data

This global vector (point) dataset models the annual expected benefits provided by mangroves to property per 20-km coastal unit, expressed as people protected per unit area (Menéndez et al., 2020). The vector dataset was spatially joined with the global mangrove grid, and summary statistics were used to calculate the mean coastal protection values within each cell. Due to the difference between our global mangrove grid and coastline intervals used in the original coastal

protection dataset, 71.7 % of cells did not receive a mean coastal protection value. Multivariate Imputation with Chained Equations (MICE) was used to estimate plausible values to gap-fill for these missing values (Van Buuren and Groothuis-Oudshoorn, 2011; Van Buuren, 2018). As per Menéndez et al. (2020), we used datasets of average astronomical tide height, maximum sustained wind speed, mangrove canopy height, mangrove basal-area weighted height and global human settlement to impute missing values. See Table S1 for details on MICE parameters and processing steps, Fig. S1 for MCMC convergence and kernel density.

2.6. Representing biodiversity

To understand minimum area-requirements to safeguard mangrove-affiliated biodiversity, we used a common target-based spatial prioritization approach focused on species representation and complementarity (Kukkala and Moilanen, 2013). We first intersected the mangrove-affiliated species ranges with the mangrove area. We created two target-setting scenarios to assign proportional protection targets for each species: 1) based on the rules of Rodrigues et al. (2004), and 2) where all species received a constant target of 30 %. The Rodrigues rules display an x-axis that is a species' total range, and a y-axis that is the proportional protection target which is relative to its range that intersects with mangroves (Fig. S2). A species with a small total range of, for example, 100 km^2 would require 100 % of its mangroves protected, whereas a species with range $> 10^7\text{ km}^2$ would require 10 % of its mangroves protected (Fig. S2). Both approaches produced similar spatial patterns, so we focus on biodiversity areas calculated using the Rodrigues et al. (2004) heuristic (although see Table S3; Fig. S3 for outputs for scenario 2). We solved for the minimum-set problem using the Integer Linear Programming tool PrioritizR, setup with a constant cost value across all grids (Hanson et al., 2017). When quantifying the number of species targets that were protected within hotspots, we performed a sensitivity analysis where we varied the allowable gap from 0 to 10 % (i.e., what proportion of the species target needed to be reached) to confirm that the representative areas were robust; see Table S6). See Table S2 for species targets.

2.7. Ecosystem service hotspot identification

Once the carbon, fisheries, and coastal protection datasets were spatially processed and gap-filled, each was normalised (0.0–1.0) and arranged in descending order. A rank from 1 to 9312 (total number of cells) was assigned to each cell for carbon and coastal protection layers. A rank from 1 to 8823 (total number of cells excluding western Africa mangrove areas) was assigned to each cell for the fish production layer. This means that the highest service provision occurs where a cell has the lowest rank value, i.e., a normalised value of 1 was ranked 1. Cells with the same normalised value receive the same rank. For single-ES hotspots, the top 10 % (ranks 1–931) of cells were identified for carbon and coastal protection. Finfish and invertebrate rank values were summed to obtain a single layer, with the lowest 882 (top 10 %) rank values extracted. To identify multi-ES hotspots, the ranks for each combination of layers were summed and then the lowest 931 (top 10 %) rank values were extracted. However, when multi-layer hotspot combinations contained the fisheries layer, the lowest 882 (top 10 %) rank values were extracted. For example, the lowest summed rank for carbon + coastal protection = 2, the highest summed rank possible based on a total of 9312 cells = $9312 \times 2 = 18,624$.

2.8. Spatial processing and statistical analysis

Spatial processing and mapping was conducted in ArcGIS Pro (v 2.7.3, ESRI Inc. 2020) and R (v 3.6.1, R Core Team 2019) using the spatial packages 'raster' (Hijmans, 2019), 'sp' (Pebesma and Bivand, 2005; Bivand et al., 2013), and 'sf' (Pebesma, 2016). Multivariate imputation was performed using the R package 'mice' (Van Buuren and

Groothuis-Oudshoorn, 2011). All datasets used in this analysis were projected to Cylindrical Equal Area projection.

3. Results

3.1. Quantify the minimum amount of mangrove area required to nominally conserve mangrove-dependent biodiversity

Our analysis suggested that a minimum of 67 % of global mangrove area is required to nominally conserve mangrove-affiliated biodiversity ('biodiversity areas'), based on the Rodrigues et al. (2004) heuristic. This percentage closely reflects the average proportional protection target by species based on the 1404 species distribution sizes. Biodiversity areas were evenly distributed across the globe (Fig. 1), with 31 nations having 100 % of their mangrove cells identified as biodiversity areas (Table S4).

3.2. Estimate the ES co-benefits that can be delivered by securing this biodiversity

Globally, biodiversity areas captured 62 % of the total carbon stored within mangroves, 35 % of the total mangrove fish production, and 41 % of the total mangrove coastal protection benefits. The percentage of hotspots (i.e., the percentage of the top 10 % of cells by rank) that were also identified as biodiversity areas ranged between 46 and 61 % across all single- and multi-ES scenarios (Table S5). In other words, between 4.6 and 6.1 % of all cells were both biodiversity areas and hotspots across all single- and multi-ES scenarios. See Fig. S4 for single service maps.

3.3. Map opportunities where high ES values co-occur

To evaluate where high ES values co-occurred, we mapped areas that were hotspots for one, two or three ES (Fig. 2A), and separately mapped the top 10 % of cells that collectively maximised services provision based on a summed ranking approach (Fig. 2D). These two approaches produced comparable spatial distributions of hotspot areas (Fig. 2). Mangrove cells with hotspots for one of the three services existed all over the world, and many nations contained cells that were hotspots for two services (Fig. 2A). Hotspots for all three services were rare and only existed in Mexico (Fig. 2B), Vietnam and Indonesia (Fig. 2C). The hotspot in Mexico was in Laguna de Terminos, and in Vietnam the Can Gio Mangrove Forest Reserve in the Mekong Delta, two areas with important fisheries, high mangrove forest cover, and frequent tropical storms. Since there are no fish production data for western Africa, cells in this region can be hotspots for only two ES, and there were several along the coastline (Fig. 2A). Taking the second approach to identify hotspots of ES provision – whereby cells are ranked across all ES and a summed rank is used to identify the top 10 % of cells – hotspots were particularly

prevalent throughout Asia, eastern Africa, central America and South America (Fig. 2D). The countries with the highest proportion of their mangrove cells as hotspots were Peru (100 %; total cells = 2), Micronesia (50 %; 6), and Vietnam (45 %; 60; Table S4).

The hotspots for single-ES captured a significant percentage of the total global service provision. For instance, the top 10 % of the mangrove cells for carbon captured 66 % of the total carbon storage; the top coastal protection cells captured 81 % of the coastal protection benefits, and; the top fish production cells captured 77 % of fish production (Table 1). These single-ES hotspots also captured between 5 and 20 % of the total global provision of the other two services (noting a random or even distribution of ES would lead to an average of 10 % captured). The ES-pair falling well above this random 10 % – suggesting some level of spatial congruence – is coastal protection and fisheries (Table 1). Accumulation curves of service provision show that additional gains in ES benefits reduce rapidly as the number of cells protected are increased (Fig. 3). We also calculate potential trade-offs and benefits of simultaneously focusing on multiple services (e.g., the three-way ES combination in Fig. 2D). For example, while the top 10 % of cells for carbon captured 66 % of the global carbon storage and 5 % of the global fish production, focusing instead on the 10 % of cells that maximize both carbon and fish (summed rank) increased the fisheries captured to 23 %, whilst forgoing 34 % of the carbon (i.e., 66–32; Table 1).

3.4. Identify unique high value opportunities for single ES that would otherwise be missed with an exclusive biodiversity-focused approach

To understand the trade-offs and opportunity for complementarity across conservation objectives, we identified and mapped ES that would be missed if conservation efforts were to focus solely on biodiversity areas. The percentage of ES hotspots that did not intersect with biodiversity areas were similar (39 % for carbon, 44 % for coastal protection, and 42 % for fisheries), but like for high value opportunities where ES hotspots intersect with biodiversity areas, where these areas existed varied spatially among ES (Fig. 4). For example, opportunities for carbon occur across central America and Asia (Fig. 4A) and for fisheries occur primarily throughout southeast Asia (Fig. 4C). Notable clusters of potential missed opportunities – where biodiversity areas and high ES provision do not intersect – for carbon occur in Indonesia and north-western Africa (Fig. 4A), and for fisheries occur in Philippines, India and Vietnam (Fig. 4C). Both high-value opportunities and potentially missed opportunities for coastal protection are scattered globally (Fig. 4B).

3.5. Quantify national-level correlations between services to provide insight into potential opportunities for leveraging ES co-benefits within nations

Finally, we evaluate national-scale ES co-occurrence to identify



Fig. 1. Global map of the minimum amount of mangrove area required to represent all mangrove-dependent biodiversity ('biodiversity areas'). Biodiversity areas are identified using a basic prioritization and the Rodrigues et al. (2004) heuristic that estimates the proportion of the species distribution required for protection as a function of the species extent of occurrence (see Methods). Analyses are conducted using 20 × 20 km grid cells containing mangroves ('cells'). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

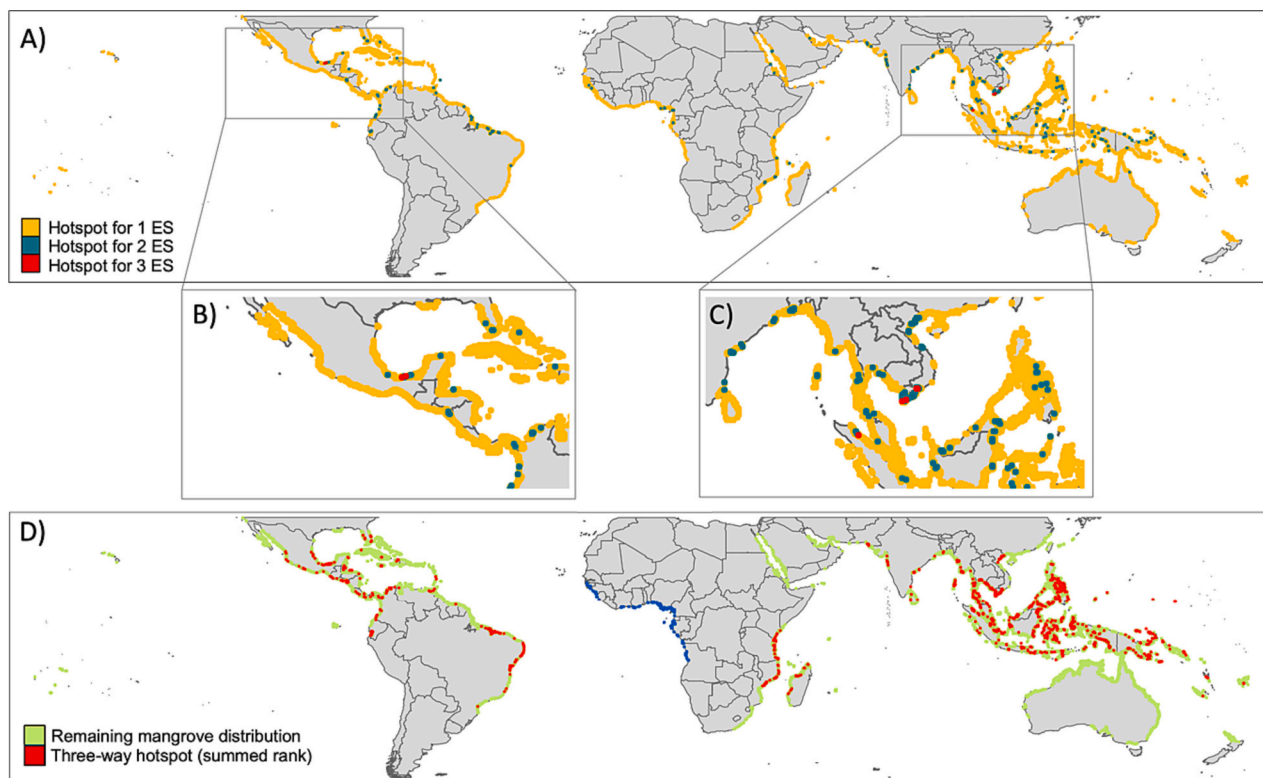


Fig. 2. Global maps of mangrove ecosystem service (ES) hotspots. (A) cells (20 × 20 km grid cells containing mangroves) that are 10 % hotspots for one or more ES (carbon storage, fish and invertebrate abundance, and/or coastal protection); (B) and (C) are inset zoomed maps with cells that are hotspots for all three ES, and; (D) cells that are hotspots (10 %) based on ranking cells to maximize all three services simultaneously (i.e., whereby cells are ranked across all ES and a summed rank is used to identify the top 10 % of cells). There is no fisheries data for west coast Africa (shown in blue for D), so hotspots within this region are based on an analysis of two services only. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Table 1

The percentage of the total global service provision captured in the 10 % hotspot cells for the individual and combined services. Darker blue reflects a greater percentage of the maximum service. Hotspots are the 10 % of cells with the highest ES provision, depending on the focal ES (i.e., rows). For rows with >1 service, hotspots are the top 10 % of cells that are hotspots (10 %) based on ranking cells to maximize all three services simultaneously (i.e., whereby cells are ranked across all ES and a summed rank is used to identify the top 10 % of cells; Fig. 2C). The analysis is based on 8823 cells due to missing fish data in western Africa.

Focal ES hotspot (10%)	Percent of global ES		
	Carbon	Coastal Protection	Fish
Carbon	66.4	8.5	5
Coastal Protection	9.8	81.1	17.5
Fish	4.6	19.9	77.4
Carbon + Coastal Protection	33.5	41.2	7.8
Carbon + Fish	32.2	16.7	22.7
Coastal Protection + Fish	6.3	44.7	39.3
Carbon + Coastal Protection + Fish	23.7	40.6	26

when national governments and organizations could more likely use conservation actions to deliver ES co-benefits (positive correlations), or where management may need to conserve multiple cells with high provision of different services in different places (i.e., ‘complementarity’; negative correlations). Vietnam, Oman, Ecuador and China showed consistent (although not necessarily strong) correlations

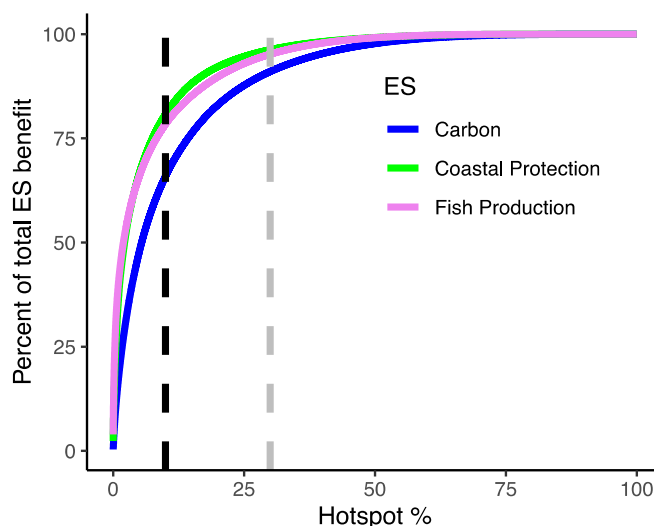


Fig. 3. Accumulation curves of the percentage of total single-ES benefit across the range of possible hotspot percentage. Dashed black vertical line shows the 10 % hotspot used for mapping here, and the dashed grey vertical line shows the 30 % related to the ‘30 × 30 initiative’ (i.e., protecting 30 % of the world’s land area by 2030; UNEP, 2020).

between ES pairs (Fig. 5). We found considerable variability among nations such that no ES pair was primarily positively or negatively correlated (Fig. 5). For instance, carbon storage and fisheries production were negatively correlated in some areas (e.g., Peru, PNG, Japan, Indonesia), but had a positive correlation in others (e.g., Ecuador, South

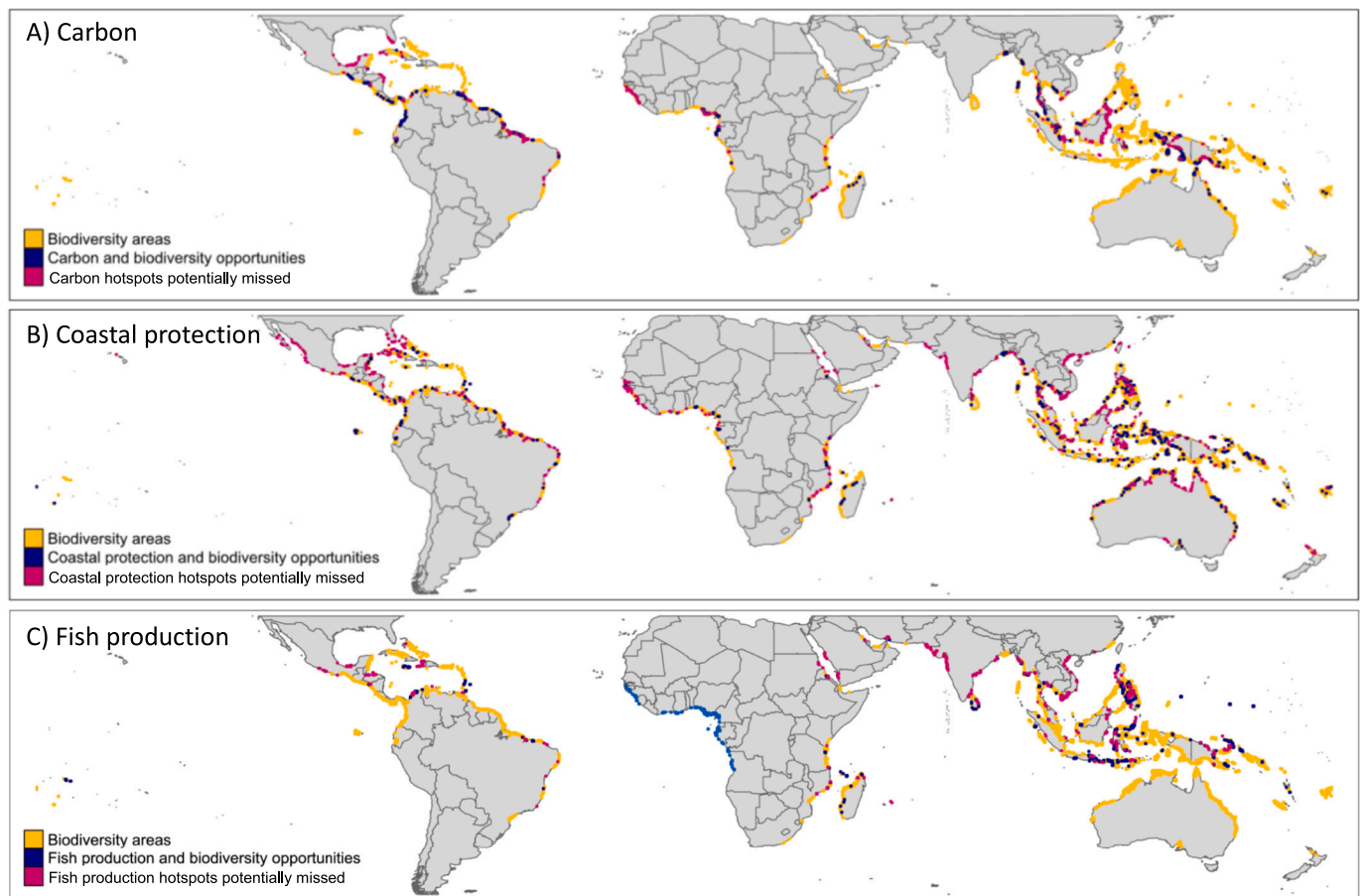


Fig. 4. Global maps showing intersections of (A) carbon, (B) coastal protection, and (C) fish production hotspots (10 %) with biodiversity areas ('opportunities'), and where ES do not intersect with biodiversity areas ('potentially missed'). Biodiversity areas are identified using a basic prioritization and the [Rodrigues et al. \(2004\)](#) heuristic that estimates the proportion of the species distribution required for protection as a function of the species extent of occurrence (see Methods). For maps using a fixed 30 % target for all species, see Fig. S3. Note there is no fish data for west coast Africa (shown in blue). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Africa, Oman, and Micronesia; [Fig. 5](#)). Nations with few mangrove cells (e.g., Peru with two cells) were only slightly more likely to show very high or very low correlation coefficients ([Fig. S5](#); see [Table S4](#) for number of cells per nation).

4. Discussion

Bringing together global datasets on mangrove-affiliated biodiversity, carbon stocks, fish and invertebrate production, and coastal protection provided insights into global trade-offs, synergies and opportunities from mangrove conservation and restoration. We found that 67 % of global mangrove area captures sufficient habitat to theoretically protect all species; an ambitious but not unachievable target ([Buelow et al., 2022](#)), and below the 80 % objective from the Global Mangrove Alliance (www.mangrovealliance.org). Of course, biodiversity is incredibly valuable for numerous reasons and across the entire mangrove distribution, so protection is needed beyond simply ensuring species do not go extinct. Our results also show that global hotspots and opportunities for single- and multi-ES scenarios exist all over the world, and that in general, most mangrove-containing nations exhibited somewhat limited spatial congruence between ES pairs.

As conservation organizations realign their goals towards meeting the needs of people in addition to biodiversity, guidance is needed to identify areas that may generate the greatest benefits among multiple ES ([Naidoo et al., 2008](#); [Doak et al., 2015](#)). This is particularly the case for mangroves, as many areas that provide high mangrove ES are

not currently protected ([Dabalà et al., 2022](#)). There is a urgency to develop and provide knowledge to support countries deliver against policy commitments they have made, including Targets 2 and 3 of the Kunming-Montreal Global Biodiversity Framework which seek to ensure that by 2030 at least 30 % of areas of degraded marine and coastal ecosystems are under effective restoration and that at least 30 % of marine and coastal areas, especially areas of particular importance for biodiversity and ecosystem functions and services, are effectively conserved and managed through ecologically representative, well-connected and equitably governed systems of protected areas and other effective area-based conservation measures.

In addition, identifying which ES are being delivered where, and highlighting where multiple ES are delivered simultaneously ([White et al., 2012](#); [Robertson et al., 2014](#); [Claes et al., 2020](#); [Lester et al., 2020](#)) can help support the implementation of policy. For instance, given the limitations of blue carbon financing at the global scale for mangroves ([Zeng et al., 2021](#)), by focusing on the multiple benefits that could potentially be delivered by conserving, restoring and sustainably using mangroves, increased political will and financing could be leveraged. ([Canning et al., 2021](#)). Similarly, by targeting restoration actions to areas which have the potential to deliver multiple benefits, the benefits to society, and the "business case" for action will be higher. Our outputs are particularly relevant given the scale of our assessment (i.e., 20×20 km cells), which falls within the spatial scale of typical mangrove restoration initiatives ([Bayraktarov et al., 2016](#)). Future work could combine our outputs with global maps of restoration potential

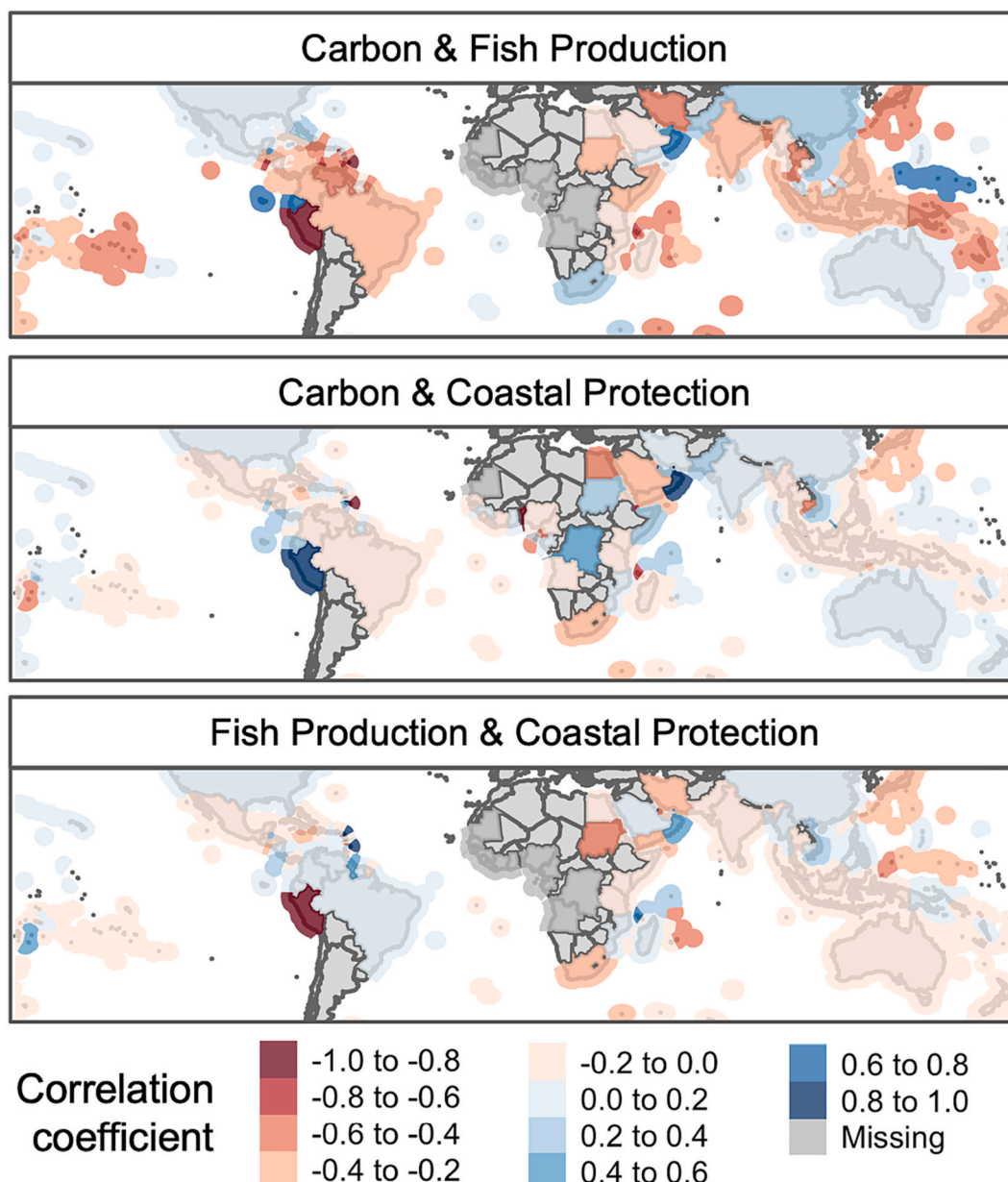


Fig. 5. Spearman rank correlation coefficients for all cells within each nation (including the Economic Exclusion Zone) for three ES pairs. Positive correlations (blue) indicate high ES congruence at cells within nations, while no or negative correlations (white to red) mean low or even no congruence (i.e., services largely occur in different cells within nations). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

(Worthington and Spalding, 2018) to identify areas that are both suitable for restoration and will likely provide high levels of ES as co-benefits.

Assessments of ES provision and biodiversity conservation at the national scale can inform subsequent analyses (e.g., prioritizations) and help nations formulate actions (e.g., protection and restoration) to accelerate progress towards meeting multiple goals under international agreements and targets (Leal Filho et al., 2018; CBD, 2020). The Kunming-Montreal Global Biodiversity Framework of the UN Convention on Biological Diversity, for instance, sets the agenda for global action to biodiversity loss. The Framework includes a goal for sustainably using and managing nature’s contributions to people, including ES (Goal B; CBD, 2022). Maps and quantification of ES and their co-occurrence can also be codified using the UN Statistical Commission’s System of Environmental Economic Accounting- Ecosystem Accounting (SEEA-EA). This is a spatially-based, integrated statistical framework for

organizing biophysical information about ecosystems, measuring ecosystem services, tracking changes in ecosystem extent and condition, evaluating ecosystem services and assets - including the economic value of mangrove ES (Taye et al., 2021) - and linking this information to measures of economic and human activity. When combined with data from the SEEA Central Framework accounts, it provides a comprehensive picture of the environmental economic relationship to support decision making (Nations, 2021; Edens et al., 2022).

Further, SDGs 14 and 15 (biodiversity conservation), 13 (climate action) and 2 (zero hunger) could all benefit from strategic efforts towards conserving areas within nations that have high service provision across biodiversity, carbon sequestration and fish production, respectively. However, given the incongruence of many mangrove services, ensuring an ES focused approach will be complemented with strategic spatial planning as well as consideration of mangrove-dependent biodiversity needs to be a priority. Where the provision of different

services is negatively correlated within a nation, conservation and management of some areas may need to look at protecting or restoring different services in different places to achieve high provision from multiple ES. For instance, coastal protection and carbon negatively correlate – albeit weakly – in many nations, including those with substantial mangrove forests such as SE Asian nations. One untested hypothesis driving this result is that mangrove forests around cities have largely been restored and contain relatively little carbon, but are still very valuable for coastal protection due to high population density. In these nations, conservation plans for these services could benefit from focusing on complementarity across different locations (e.g., Beger et al., 2015). Since other ES pairs showed high variability in spatial co-occurrence across nations, such as carbon and fish production, some nations could leverage multiple ES (e.g., China, USA) whilst others may need to focus on complementarity (e.g., Mexico, Brazil, SE Asian countries). Even in these former nations, however, individual sites such as Laguna de Terminos in Mexico, can still provide useful opportunities to leverage co-benefits. Indeed, given the spatial scale of our analysis, small-scale and strategic local action that identifies and leverages multiple benefits would likely be possible in many places. Ultimately, the location, timing and action-set (e.g., restoration, protection, or improved management) needs to be determined at appropriate scales given enabling conditions, local impacts on communities, and stakeholder engagement and values (Chaplin-Kramer et al., 2021; Tallis et al., 2021; Fleischman et al., 2022). Our national scale correlations can inform decision-making and provide a first cut towards on-the-ground action.

4.1. Caveats and assumptions

There are important caveats and assumptions in our analyses. First, the ES layers are based on data from different points in time, but we assume they are comparable and represent the ‘present day’ state. Second, we assume our gap-filling approaches are suitably accurate, particularly for coastal protection where due to the nature of the dataset, 71.7 % of cells did not initially receive a mean coastal protection value. However, we utilised an approach – Multivariate Imputation with Chained Equations – that incorporates the same accompanying data layers used by Menéndez et al. (2020) to estimate plausible values for coastal protection for the missing cells, and interrogated the robustness of this analysis (Table S2). Third, particular conservation actions can have conflicting outcomes for different ES (e.g., protected areas can conserve carbon but reduce access for fisheries; Di Franco et al., 2016). This means that overall service provision for some ES pairs may in practice be lower than presented here. Given the lack of comprehensive global mapping of fishing restrictions, for example, calculating any such reductions is beyond the scope of this work. Fourth, our approach does not consider the level of threat mangroves are facing within each cell, nor the ecological condition of the mangroves at fine spatial scales; these could have important implications for conservation decisions and actions. Fifth, we reiterate the absence of fish data in West Africa, meaning that for some analyses and maps, this area was unable to have certain hotspots. This does not suggest west African mangroves are less important, and indeed several cells along this coastline were hotspots for both (all) their currently mapped ES. Effort should be made to include these areas in future models of fish production, and subsequent ES asset maps.

Decisions with respect to the species list or prioritization algorithm can modify cells identified as ‘biodiversity areas’, and thus the outputs should be viewed as one way to achieve a set of conservation objectives. Since the costs of potential conservation actions are not available at a global scale (Iacona et al., 2018), we followed common practice in global optimizations and focused only on understanding the minimum area required to safeguard mangrove-dependent biodiversity and placed no additional constraints on the analyses such as costs or likelihood of conservation success. Further, many of the species included naturally

use habitats other than mangroves, which themselves are likely to be under various levels of protection and threat, and thus protecting the assigned biodiversity areas does not ensure all species will be conserved, nor does protecting less than our areas suggest they won’t be. We therefore use biodiversity areas not as a map of irreplaceable biodiversity for mangroves, but rather as a way to ensure adequate biodiversity representation and to explore potential co-benefits at global scales. Future work would benefit from evaluating how much of the dependency per species relies on mangroves, and from approaches that assess biodiversity representation based on changes in how much of a species’ range is located in protected areas, such as the species protection index (Jetz et al., 2022).

4.2. Looking forward

Identifying where investment can maximize positive outcomes for multiple ES is an important first step to informing conservation and restoration actions for mangrove ecosystems (Claes et al., 2020), and global analyses can make several contributions towards priority setting and decision making (Chaplin-Kramer et al., 2021). Since our biodiversity areas and ES hotspots do not account for local conditions, permissions, cost-effectiveness, stakeholder values, or national priorities, they do not necessarily identify the best or most suitable areas for conservation and restoration. Nevertheless, in providing these maps and analyses, we identify areas where leveraging multiple ES benefits may be most achievable versus where seeking areas that are complementary for different services may be most desirable. A next step would be to use information on the spatial distribution of ES within quantitative prioritization tools to inform action planning (Tallis et al., 2021). Such prioritizations should be conducted in partnership with agencies that are funding conservation because outcomes of priority maps are most meaningful when the objectives (e.g., carbon only versus multiple services) and scale of conservation actions are clear (Game et al., 2013). Prioritizations also need to consider additional information on feasibility, opportunity costs, and local and cultural needs (Brown et al., 2015) and such information is not yet available at global or even (most) national scales for mangroves (although see Adame et al., 2015, Atkinson et al., 2016, Rahman et al., 2021). Future work should integrate the preferences and values of stakeholders and indigenous peoples and local communities. Such preferences inevitably inform priorities and result in more equitable and just outcomes. Finally, future maps could also evaluate where hotspots intersect with, for example, areas of high mangrove loss (Hamilton and Casey, 2016), mangrove fragmentation (Bryan-Brown et al., 2020), protected areas (UNEP-WCMC, 2020), cumulative impacts (Turschwell et al., 2020), or wetland status (Sievers et al., 2021).

5. Conclusions

Generating and evaluating asset maps of biodiversity and ecosystem services (ES) is an important precursor to identifying the most appropriate actions to deliver conservation and restoration outcomes across varying scales. By bringing together global datasets on three mangrove ES and data on mangrove-affiliated biodiversity, we provided insight into potential trade-offs, synergies and opportunities from mangrove conservation. A lack of clear or consistent spatial trends suggests that some nations will likely benefit more from complementarity-based approaches, whilst others could best achieve progress towards key conservation and restoration goals and targets by focusing on areas with high ES co-occurrence. Whilst decisions about where and how to conserve and restore ecosystems is contingent on social, political, economic and ethical considerations, our work provides a useful step to informing these analyses and decision-making.

CRedit authorship contribution statement

Michael Sievers: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Christopher J. Brown:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – review & editing. **Jennifer McGowan:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Mischa P. Turschwell:** Investigation, Methodology, Writing – review & editing. **Christina A. Buelow:** Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. **Briana Holgate:** Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. **Ryan M. Pearson:** Investigation, Methodology, Writing – review & editing. **Maria F. Adame:** Investigation, Methodology, Writing – review & editing. **Dominic A. Andradi-Brown:** Investigation, Methodology, Writing – review & editing. **Andy Arnell:** Investigation, Methodology, Writing – review & editing. **Brendan G. Mackey:** Investigation, Methodology, Writing – review & editing. **Philine S.E. zu Ermgassen:** Investigation, Methodology, Writing – review & editing. **Joe Gosling:** Investigation, Methodology, Writing – review & editing. **Chris J. McOwen:** Investigation, Methodology, Writing – review & editing. **Thomas A. Worthington:** Investigation, Methodology, Writing – review & editing. **Rod M. Connolly:** Conceptualization, Funding acquisition, Investigation, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare no conflicts of interest.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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