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Minimizing cross-realm threats from land-use change: A national-scale conservation framework connecting land, freshwater and marine systems

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ABSTRACT

There is a growing recognition that conservation strategies should be designed accounting for cross-realm connections, such as freshwater connections to land and sea, to ensure effectiveness of marine spatial protection and minimize perverse outcomes of changing land-use. Yet, examples of integration across realms are relatively scarce, with most targeting priorities in a single realm, such as marine or freshwater, while minimizing threats originating in terrestrial ecosystems. To date, no study has optimized priorities across multiple realms to produce a spatially explicit integrated conservation plan that simultaneously accounts for multiple human activities at a national scale. This represents a major gap in the application of existing cross-realm planning theory. We present a national scale conservation framework for selecting protected areas using a case study of Papua New Guinea (PNG) that integrates multiple systems and ecological connectivity to account for cross-realm benefits and minimize threats of land-use and climate change. The relative importance of both the forests and inshore reef environments to PNG subsistence and commercial livelihoods emphasizes the importance of considering the connections between the land and sea. The plan was commissioned by the PNG Conservation and Environment Protection Authority and identifies a comprehensive set of priorities that meet conservation targets in both the land and sea. Our national-scale prioritization framework is useful for agencies and managers looking to implement actions given multiple objectives, including watershed management and biodiversity protection, and ensures actions are efficient and effective across the land and sea.

1. Introduction

Threats to biodiversity span multiple realms, such as clearing on land that affects both terrestrial ecosystems and connected freshwater and coastal marine ecosystems from increased erosion and sedimentation (Álvarez-Romero et al., 2011; Stoms et al., 2005). Although protected areas remain a cornerstone of conservation strategies to combat ongoing biodiversity loss (Bertzky et al., 2012; Butchart et al., 2010), the impacts of cross-realm threats or otherwise displaced drivers such as climate change can undermine the effectiveness of conservation interventions. Thus, it is critical to design conservation strategies, and in particular protected areas, that take into account connections across multiple realms and include likely change (Adams et al., 2014; Álvarez-Romero et al., 2015a; Álvarez-Romero et al., 2011).

Despite increasing recognition that conservation strategies should account for cross-realm connections, examples of integration across realms that include climate impacts are relatively scarce (Álvarez-Romero et al., 2015a). Most examples target priorities in a single realm,

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such as marine (Tallis et al., 2008) or freshwater (Linke et al., 2007). Although single-realm focused decision-making can achieve local-scale objectives efficiently, they may be ineffective in protecting biodiversity (Tulloch et al., 2016). This is because changing land-use, whether through development or conservation, has wide-reaching indirect impacts on connected freshwater and marine ecosystems. Only a few studies have integrated priorities for management across realms, and typically, they allocate actions within a single realm but account for benefits across multiple realms, often in an iterative rather than integrated manner (Álvarez-Romero et al., 2015b; Klein et al., 2010; Klein et al., 2014; Tulloch et al., 2016). Previous research shows that ignoring connections in conservation plans delivers substantially different spatial priorities compared to approaches that are integrated and connected (Makino et al., 2013; Tsang et al., 2019). To date, no study has optimized priorities simultaneously across multiple realms to produce a spatially explicit integrated conservation plan for connected terrestrial and marine conservation priorities given multiple threats including future change (but for a review of existing approaches see Adams et al., 2014; Álvarez-Romero et al., 2015a). This represents a major gap in conservation planning theory.

Potential reasons for the lack of fully integrated cross-realm conservation plans that account for multiple threats include barriers in data availability or technical capacity in existing optimization approaches (Adams et al., 2014; Álvarez-Romero et al., 2015a). However, both of these barriers are rapidly diminishing. For example, global data sets of watershed boundaries and sub-basin delineations are now available to support planning and prioritization efforts at global scales (e.g., HydroSHEDS, Linke et al., 2019). They allow for analysis of up- and downstream connectivity (Allan et al., 2019; Hermoso et al., 2012). Multiple tools that assist both understanding and modelling runoff regimes are available, even for data-poor regions (Brown et al., 2019). Models for dispersion of pollutants and sediments in the ocean range from putative representation of threat impacts using relative indices (Halpern et al., 2009) to hydrodynamic modelling that explicitly link dispersal and transformation of pollutants to ocean processes (Wolff et al., 2018). There have also been advances in optimization approaches to support cross-realm planning (Cattarino et al., 2018; Cattarino et al., 2015; Tsang et al., 2019; Wenger et al., 2020). Despite the increased availability of these data, tools and frameworks, the majority of coastal marine protected area (MPA) planning is still conducted without consideration of adjacent and upstream land-use, nor of likely land-use change.

We present a national-scale systematic conservation framework that integrates multiple systems, multiple threats and cross-realm connectivity to account for cross-realm benefits that minimize the chance of protecting inefficient degraded areas. We use Papua New Guinea (PNG) due to its globally significant biodiversity, rapidly accelerating threats, and the connected nature of the terrestrial and marine ecosystems (e.g., the Fly and Sepik rivers represent globally significant river discharges). The relative importance of both the forests and inshore reef environments to PNG subsistence and commercial livelihoods emphasizes the importance of considering the connections between the land and sea. Ridge-to-reef planning aims to connect the protection of terrestrial, coastal and marine habitats in order to ensure that forests that are upstream of important coral reefs or coastal habitats are intact, and therefore support the flows between upstream and downstream conservation values. Our framework expands on previous land-sea conservation research developed by Tulloch et al. (2016), by including asymmetric connections between catchments on the land and marine planning units, and prioritizing both realms simultaneously. We use our new framework to identify areas of conservation priority across land and sea, accounting for asymmetric connectivity between realms. To demonstrate the accessibility of the approach, we conduct individual land and sea prioritizations to quantify the extent to which optimizing priorities jointly changes spatial distribution and potential impacts on efficiency of conservation plans. We discuss the use of existing data products that we utilized, that are freely available, and can support this approach in other regions, particularly those that are data-poor or have limited technical capacity.

2. Methods

2.1. Case study region

PNG has a land area of 461,690 km^2, encompassing tropical forests, savannah grass plains, big rivers and deltas, swamps and lagoons, and numerous islands and atolls to the east and north east of the country. The main island of New Guinea supports an estimated 5–9% of the world's terrestrial biodiversity on less than 1% of its land area (Mittermeier et al., 1998). Similarly, the marine environment of PNG is highly diverse and productive; PNG waters are considered part of the Coral Triangle, which contains the world's highest marine biological diversity. Its coral reefs and associated marine habitat are home to about 2800 species of fishes, about 10% of the world total (Randall, 1998).

Over 80% of PNG's population is dependent on subsistence agriculture for food, and increasingly, small scale cash crops which results in increased rates of forest conversion and degradation (annual rate of degradation of 1.41% (Shearman & Bryan, 2011). Similarly, PNG's industries such as mining, forestry and palm oil, are rapidly expanding, and all result in forest conversion and increased pollutants in water ways. Cross-realm conservation has been identified as a critical research gap stemming from outcomes of previously developed single-realm plans for land (Lipsett-Moore et al., 2010) and the ocean (Marine Gap Analysis, Government of Papua New Guinea, 2015).

2.2. Land-sea prioritization approach

One approach to planning for land-sea connections is to prioritize land areas with lower erosion (i.e. intact forests) so that these forests continue to provision downstream ecosystem services such as (reduced) land erosion, clean water, and connectivity for freshwater and marine fish (e.g., Álvarez-Romero et al., 2015b). This approach is simplistic as it does not simultaneously connect and prioritize intact terrestrial and marine areas, but instead aims to minimize land-sea threats by protecting low erosion sub-catchments. Similarly, marine planning approaches may consider the downstream impacts of runoff from development (e.g. Tulloch et al., 2016), but do not account for the simultaneous benefits of land conservation.

A more sophisticated approach to ridge-to-reef planning is to explicitly include both the impacts of erosion and runoff in the marine realm, and upstream benefits of land protection to avoid runoff. Asymmetric land-sea connectivity allows directional connections between catchments and marine planning units to be considered, thus more effectively capturing true ecological and locational connectivity (Beger et al., 2010b). For example, if a reef is prioritized, then connected upstream catchments are more likely to be prioritized. Similarly, if a catchment is selected, it will impact the selection of nearby reefs. This requires the integration of outputs from erosion and runoff modelling, and ocean dispersal of sediments, within a spatial prioritization framework.

2.3. Marxan with land-sea connectivity

To account for asymmetric land-sea connectivity, we developed a new framework that uses Marxan with Connectivity, an extension of the popular decision-support tool Marxan (Ball et al., 2009a). Marxan is an area selection algorithm that finds priority conservation areas given their cost-effective contribution to achieving biodiversity targets. In standard Marxan, only connectivity in the form of spatial adjacency between planning units can be considered in the form of a "boundary length modifier" (BLM), which allows final solutions to be clumped. Marxan with Connectivity allows planners to consider asymmetric connectivity by including an additional user-defined connectivity "cost" in their prioritization (Beger et al., 2010b), to link planning units that may not be spatially adjacent but connected ecologically. The steps for including land-sea connectivity in spatial conservation planning are: 1) Identify conservation goals, 2) Identify biodiversity features, 3) Define scale of action, 4) Set targets, 5) Identify connections, 6) Define costs and constraints and 7) Spatial prioritization using Marxan with Connectivity. We describe the process below and in Fig. 1.

1. Step 1: Identify conservation goals and objectives

To optimally prioritize actions across land and sea realms, it is essential to clearly state the highest priority objectives (Possingham et al., 2001). These objectives could be driven primarily by threatened species conservation, or managing existing pressures, or exploring new development options (e.g., Tulloch et al., 2016), depending on the region and the needs of the stakeholders. Our objectives were defined in consultation with the PNG Government, and covered local, cross-realm and global objectives: represent marine habitats and important areas for threatened or high value species (fish spawning aggregations, critical habitats for whales, seabirds and sea turtles); represent land habitats, endemic or threatened terrestrial fauna, and climate refugia; and incorporate asymmetric riverine connectivity to protect land catchments with low deforestation whilst avoiding coastal areas that may contain degraded reef ecosystems from runoff (Fig. 1).

2. Define the scale of conservation actions

To allocate actions spatially, the planning region should be divided into a number of planning units, the size and dimensions of which are user-defined. If spatial conservation planning has already been conducted in the region, units developed previously could be used for expediency and consistency. Land-sea runoff modelling is typically conducted at the scale of watersheds and sub-watersheds, however, so these may be a more efficient planning unit choice for land actions as the results of hydrodynamic models can be readily transferred to each planning unit. If other units were chosen for actions on the land (such as property cadasters, or traditional tenure), transferring outputs from

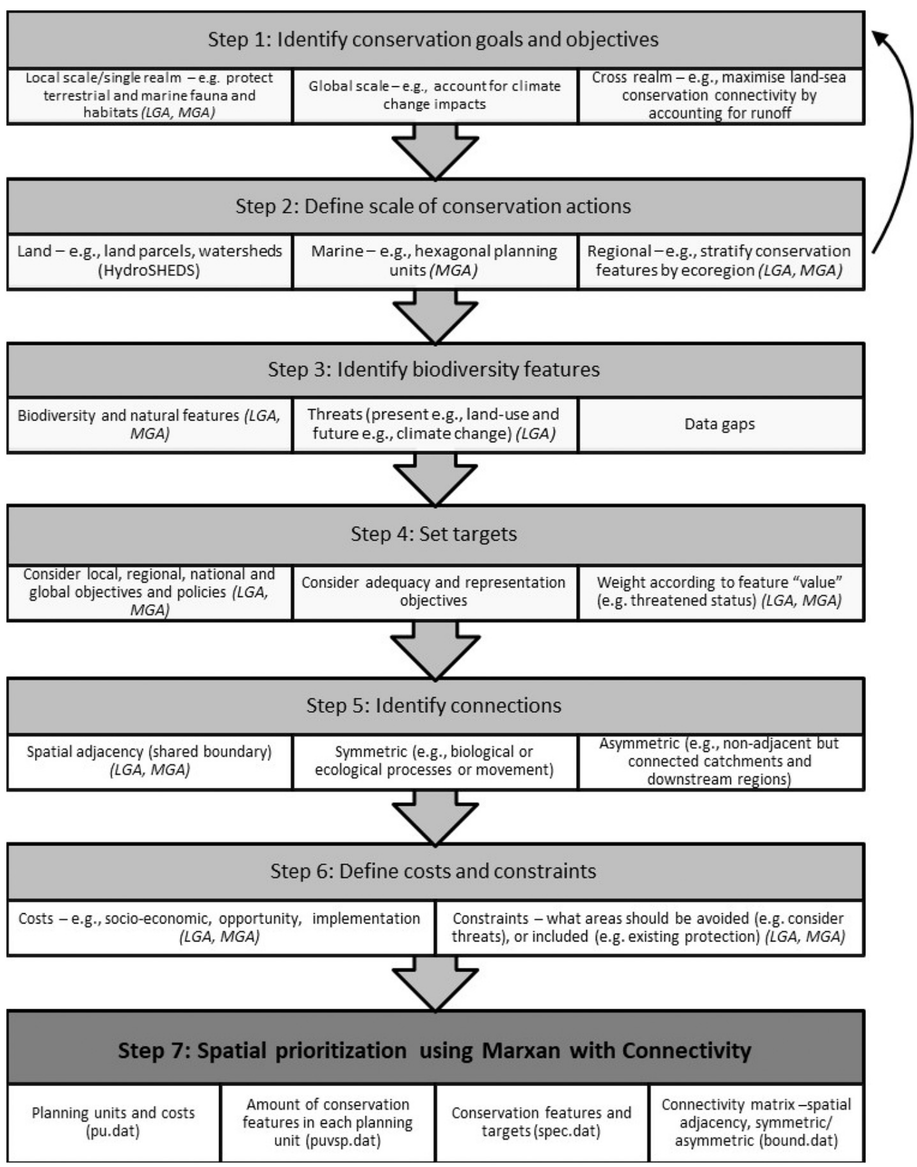

Fig. 1. Flowchart of steps for including land-sea connectivity in spatial conservation planning: 1) Identify conservation goals, 2) Define scale of action, 3) Identify biodiversity features, 4) Set targets, 5) Identify connections, 6) Define costs and constraints, and 7) Spatial optimization using Marxan with Connectivity. We also note in the boxes where previous research has been used to inform objectives, scale, targets and constraints (MGA = Marine Gap Analysis, LGA = Land Gap Analysis).

runoff models would require spatial interpolation to the new scale of the planning unit boundary.

For terrestrial planning units, we used the HydroBASINS watershed boundaries for Papua New Guinea created by HydroSHEDS (http://www.hydrosheds.org/page/hydrobasins). HydroSHEDS and the associated HydroATLAS database provides open-source readily available data on catchments, river flow, and other processes necessary as data inputs for the land-sea model (Linke et al., 2019). Using the HydroSHEDS database at 15 arc-second resolution, watersheds were delineated in a consistent manner at different scales, and a hierarchical sub-basin breakdown was created following the topological concept of the Pfafstetter coding system (see Stein, 2018). There were a total of 3301 sub-catchments in our terrestrial planning unit layer, with an average area of 14,400 ha.

For the marine region, we used the same hexagonal planning units employed in the Marine Gap Analysis (Government of Papua New Guinea, 2015). The EEZ of Papua New Guinea was divided into 50,215 hexagonal planning units encompassing both deep and shallow water habitats and adjacent coastal areas where mangroves were present. Each hexagon had an area of 5000 ha; a size deemed appropriate for both the scale of the analysis and the computing and processing time required by Marxan. Given the coastal land-sea focus of our framework, we locked in all priority areas identified in the previous Marine Gap Analysis that were offshore and constrained our analysis to those marine planning units in the coastal shelf.

The final step in defining the scale of conservation actions is to calculate the amount of each conservation feature in each planning unit. We stratified features by bioregions and ecoregions, defined in previous national-scale prioritizations for land (Lipsett-Moore et al., 2010) and marine environments (Government of Papua New Guinea, 2015; Green et al., 2014) (Fig. 2).

3. Identify conservation features

To represent the biodiversity of a region, spatial data should be collected and mapped on biotic and abiotic features including biological (e.g., species, communities, habitat types, critical habitat) and physical (e.g., geology, climate) attributes. To avoid bias in final spatial outputs, only data that covers the whole study region should be used. Data can be obtained from online sources (e.g. IUCN Red List of Threatened Species, https://www.iucnredlist.org/), data repositories, as well as previous conservation plans, whilst proprietary data such as fisheries effort or the locations of culturally important sites are typically obtained from stakeholders.

For the terrestrial environment, we included coarse filter data of land-use cover and habitat types, climate refugia, and special features including distributions of endemic and threatened species, as previously used in the land gap analysis (Lipsett-Moore et al., 2010) (Table 1, for a full description of datasets and targets see Supplementary methods and Tables S1–S3). For the marine environment, we included biophysical data on geomorphology, critical habitat for threatened bird, turtles and marine mammals, and reef fish spawning sites, as previously used in the marine gap analysis (Government of Papua New Guinea, 2015) (Table 1, Table S3).

4. Set targets

Conservation targets should align with regional, national or global conservation policies and objectives (e.g., signatories to the United Nations Convention on Biological Diversity (CBD) are required to meet spatial protection targets of at least 10% of coastal and marine areas and 17% of terrestrial areas in protected areas to slow the global loss of biodiversity (Convention on Biological Diversity, 2010)). Features can

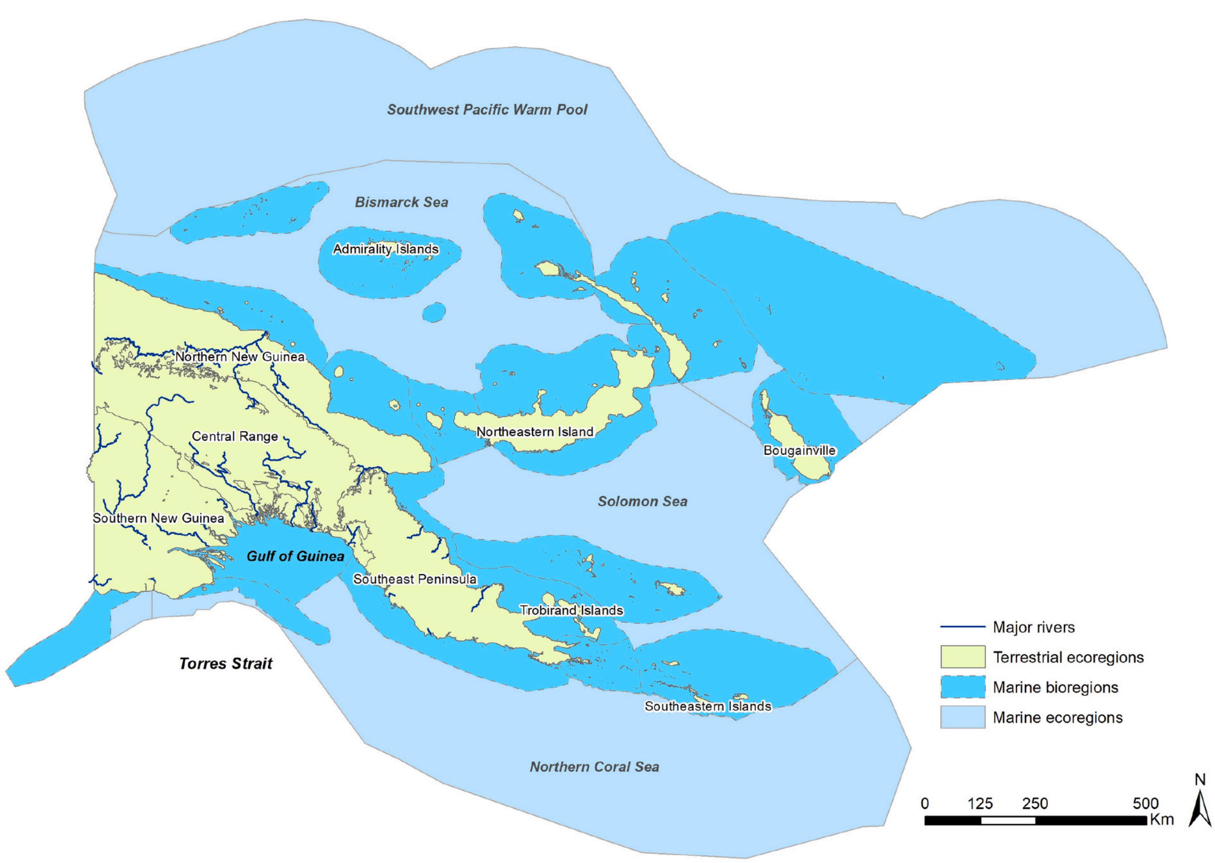

Fig. 2. Study area highlighting terrestrial ecoregions (Lipsett-Moore et al., 2010), marine bioregions and ecoregions (Government of Papua New Guinea, 2015; Green et al., 2014), and major rivers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Description of conservation features, associated data set, and targets for terrestrial and marine ecosystems.

Realm	Type	Description	Number features	Target
Terrestrial	Land systems	Abiotic land systems (81) stratified by ecoregions	359	A 10% target was set for each abiotic land system class across Papua New Guinea.
Terrestrial	Vegetation	Natural vegetation types (61 total: 36 Forests, 6 Woodland, 3 Savanna, 3 Scrub, 11 Grasslands, 1 Mangrove and 6 Non Vegetation Types) stratified by percentage disturbed and by ecoregion.	954	A 10% target was set for any natural vegetation type (e.g., forested, grassland, etc) in keeping with the previous POWPA, stratified by each ecoregion. No targets were set for developed classes (e.g., bare, oil palm, timber plantation).
Terrestrial	Fauna - Restricted Range Endemic Species	Restricted Range Endemic Species including Bird of Paradise (10), Tree Kangaroos (12), Reptiles and Amphibians (123), Mammals (25)	170	Recognizing that restricted range endemic species are only found at a single site, these species were given 50% targets.
Terrestrial	Fauna - Critically Endangered and Endangered terrestrial species	IUCN RedList Critically Endangered and Endangered terrestrial species ranges including mammals (27) and amphibians (1).	28	Given the coarse resolution of this data and large spatial extent for most of these features we applied a 5% target. Given the large ranges, sensitivity tests for these features revealed most met their representation targets in the prioritizations without requiring actual targets to be set.
Terrestrial	Climate refugia	Climate refugia	1	We used a threshold approach, where planning units with a probability of less than 0.25 (>25% chance of acting as a climate refugia) were targeted 5%.
Marine	Biophysical habitat data	Habitat conservation features (oceanic geomorphological features (19), depth class (7), coastal mangroves (1), nonreef shallow shelf (1), coral reefs (169)) stratified by marine bioregion and ecoregion.	1575	We set a goal of 10% for all habitat conservation features stratified by marine bioregion and ecoregion. This reflects the CBD target of 10% protection for marine habitats.
Marine	Fauna	Areas important for shorebirds and seabirds (Beck's Petrel, Streaked Shearwater, Heinroth's Shearwater, Rednecked Phalarope, Brown and Black Noddy, Greater Sand Plover), Blue whale critical breeding sites, Sperm whale historical catches, Green turtle	10	A 20% target was set for each of these special features.

be given different weights according to their "value" (e.g., one might wish to assign endemic or threatened species elevated conservation priority) (Arponen et al., 2005; Carwardine et al., 2009). The concepts of adequacy, or the ability of conservation measures to conserve biodiversity, should be considered in the setting of targets (Carwardine et al., 2009).

Our overall goal was to protect approximately 20% of PNGs marine and terrestrial environments, by differentially weighting conservation features (Table 1). Targets were defined iteratively based on discussions with stakeholders. We targeted features at national and regional scales (Table 1), using ecoregions and bioregions defined in the previous national-scale prioritizations for land (Lipsett-Moore et al., 2010) and marine environments (Government of Papua New Guinea, 2015) (Fig. 2).

5. Identify connections

The most important step in the land-sea prioritization is to identify, model and quantify connections. It is possible to include several types of connectivity in the advanced Marxan tool, for example, locational connectivity (e.g., forest corridors, reef complexes), biophysical connectivity (e.g. ridge-to-reef), and ecological connectivity (e.g., migratory routes, dispersal).

Here, we included 3 types of connectivity:

1) riverine connectivity of our terrestrial planning units,
2) marine connectivity of our marine planning units, and
3) land-sea connections between our terrestrial and marine planning units taking into account freshwater runoff and plume modelling.

For riverine connectivity we used asymmetric connectivity based on freshwater sub-catchment connections, as detailed in Linke et al. (2012). For marine connectivity, we included shared boundaries of marine planning units, as this is the standard method for including connectivity in marine conservation planning. Other types of connectivity that could be considered in the marine realm include biological processes such as dispersal and larval connectivity (Beger et al., 2010b; White et al., 2014), fish spawning and aggregation connections (Beger et al., 2015), physical characteristics such as ocean circulation patterns (Magris et al. 2016), seascape or ecosystem connectivity (Mumby, 2006), and migratory pathways (Beger et al., 2015). Land-sea connections require spatial information on terrestrial erosion and sedimentation levels across a region, and associated downstream outputs of sedimentation and other pollutants transport from the land into coastal waters. This can be obtained from existing hydrodynamic, erosion and sediment models, if such outputs are available. If not, this information must be derived, by using in-situ data or remote sensing (e.g., Rodríguez-Guzmán and Gilbes-Santaella, 2009) or developing new models (see Merritt et al., 2003 for a comprehensive review).

Here, we developed a land-sea runoff and ocean dispersal model based on previous work by Tulloch et al. (2016), expanding to a national scale. We used the open-source version of the runoff simulation tool N-SPECT (Nonpoint Source Pollution and Erosion Comparison Tool) (Eslinger et al., 2005) in MapWindow GIS to simulate runoff and sediment discharge from watersheds at river pour points. N-SPECT combines data on elevation, slope, soils, precipitation, land cover characteristics, as well as surface retention and abstraction (USDA, 1986), to derive estimates of runoff, erosion and pollutant sources (nitrogen, phosphorous and suspended solids), and accumulation in stream and river networks (data sources and transformations for N-SPECT parameterization described in Supplementary Methods, and see Tulloch et al., 2016). We applied an existing plume model (Halpern et al., 2008) for those rivers with runoff values above 5^{e9}L/yr. We spatially calculated the accumulated sediment from the N-SPECT output at each river mouth for each scenario. A simple linear regression model was used to fit the distance of a plume per river discharge in the statistical computing software, R; the resulting function was applied to calculate the plume distance from river mouths.

6. Identify costs and constraints

Efficient conservation planning considers the relative costs of spatial action across a landscape (Naidoo et al., 2006). Cost metrics can be derived from a variety of different sources, depending on the management objectives and available data (Carwardine et al., 2008), and are often based on spatial socioeconomic data (Ban and Klein, 2009). On the land, this might be based on land acquisition or stewardship costs (Carwardine et al., 2008), or proxies of human presence. In marine environments, costs might be derived from opportunity costs to fishers, or other proxies of human resource use (Ban and Klein, 2009), or transaction costs (Gissi et al., 2018). Other metrics could include the cost of obtaining data (Tulloch et al., 2017), feasibility metrics (Jones et al., 2018; Tulloch et al., 2014), or implementation and management capacity.

Our land cost surface layer was initially derived from a previous terrestrial conservation plan for the region (Lipsett-Moore et al., 2010), which used socio-economic information as a proxy for cost of protection based on the 2000 population census data for Papua New Guinea (NSO, 2011). Each population census point was summed to provide a total population value for each hexagon. This provides the appropriate gradient for Marxan to work with, from populous areas where it is expensive to create and manage protected areas, to less populous areas where it is less expensive to create and manage protected areas and where human threats tend to be lower. For the marine cost surface, we used a surrogate for fishing pressure to represent the lost opportunity costs of conservation, based on the same distance landings-weighted cost model used in the previous Marine Gap Analysis (Government of Papua New Guinea, 2015). The relative cost of conservation was determined in terms of the opportunity cost to fisheries, calculated by determining the distance of each planning unit from ports, weighted by fisheries landings at those ports. Once combined, we standardized the marine and land cost values so that bounds were comparable.

In order to avoid areas of high conflict we locked out areas identified as having existing or proposed mines, oil and gas. These were identified by buffering point data for these sites with a 5 km buffer and locking out any catchments contain more than 25% mining oil or gas sites. We also avoided major towns and villages. We used the census data to create buffers around all towns in PNG proportional to the population, with a maximum buffer of 10 km around the biggest villages. We assigned any catchments with >25% of their area containing village buffer as unable to be selected for conservation priority (locked-out).

7. Spatial prioritization using Marxan with Connectivity

The final step is to run Marxan with Connectivity to find priority conservation areas that account for ecological linkages. There are several options for running Marxan with Connectivity, including running from source code, software (https://marxansolutions.org/software/), or using 'Marxan Connect' (https://marxanconnect.ca), a new open source, open access Graphical User Interface (GUI) tool (Daigle et al., 2020).

As Marxan is a decision-support tool, it can be used to compare outputs of different planning scenarios (Daigle et al., 2020). Here, we considered three planning scenarios. The first scenario was based on single-realm land conservation planning that aimed to avoid erosion solely on the land, ignoring cross-realm connectivity and marine processes (hereafter "land-focused" scenario, Table 2). The second scenario considered runoff from the land in marine priorities alone, and did not prioritize terrestrial regions (hereafter "marine-focused" scenario), similar to that used in recent conservation plans (e.g., Delevaux et al., 2018; Tulloch et al., 2016). The third was the new asymmetric land-sea prioritization, that optimizes priorities for both marine and terrestrial regions together. This shifts marine priorities to ensure that connected terrestrial, coastal and marine habitats are protected, where possible in lower erosion catchments (hereafter "cross-realm" scenario, Table 2).

We parameterized Marxan for each scenario without representing any asymmetric connections between planning units (hereafter "Standard" approach, Ball et al., 2009b), and then included biophysical connectivity into the objective function ("Connectivity" approach, Beger et al., 2010a; Beger et al., 2010b; Daigle et al., 2020) (Table 2).

The cross-realm and marine-focused scenarios include the outputs of the ridge-to-reef runoff model, which accounts for the chance of marine ecosystem degradation due to deforestation and agriculture. For these two scenarios, we used a thresholds approach to prioritizing marine planning units based on level of threat (or runoff) in each planning unit. We tabulated statistics for all marine planning units where there was predicted runoff, including average, minimum, maximum, and total summed accumulated sediment, and used these to set thresholds for avoiding runoff in coastal waters. Given that Papua New Guinea has high levels of natural runoff and sediment entering coastal waters due to high rainfall and steep topography, we used an approach which accepts a certain level of risk. To this end, we allowed areas with low to medium levels of runoff to be included in the prioritization. We calibrated the threshold for sediment by comparing plumes with Landsat images between 2012 and 2014 for Papua New Guinea, and chose a minimum accumulated sediment threshold of 5,000,000 T. To help ensure the selected network comprised a compact set of protected areas, we utilized the boundary length modifier (BLM) function within Marxan.

For each scenario we ran Marxan to identify spatial priorities to meet our conservation targets and connectivity objectives for the lowest possible cost (Ball et al., 2009b). We kept the same number of iterations (10,000,000), runs (100) and the associated cost consistent in all planning approaches. The best solution (the one with the minimum objective function score) and selection frequency (i.e. number of times a planning unit was selected across the 100 solutions) were compared between scenarios. The "selection frequency" refers to the frequency that an individual cell is selected across the 100 solutions. This gives an indication of its importance in meeting representation targets and achieving an efficient reserve network, and is commonly used to identify high priority conservation areas (Possingham et al., 2000). Difference maps were used to compare how the location of priority areas would change when we used different constraints, by subtracting the planning unit selection frequency of one scenario from the other. We calculated the total proportion of each conservation feature in each ecoregion and bioregion to

Table 2
Description of planning scenarios.

Scenario	Targets and objectives	Land prioritized	Marine prioritized	Erosion	Runoff	Connectivity approach
Land-focused standard	Land features only	x				Adjacency only (BLM)
Land-focused connectivity	Land features, land processes - avoid erosion on land	x		x		One-way - from upstream catchment to downstream catchment
Marine-focused standard	Marine features only		x			Adjacency only (BLM)
Marine-focused connectivity	Marine features and land processes - avoid runoff plumes		x	x	x	One-way - from river mouth to marine planning units
Cross-realm standard	Land and marine features	x				Adjacency only (BLM)
Cross-realm connectivity	Land and marine features, avoid erosion on the land and runoff in marine reserves	x	x	x	x	Two-way asymmetric connectivity between terrestrial and marine planning units

analyze representation of conservation features in each prioritization scenario.

3. Results

The ‘standard’ land-focused scenario identified spatially sparse priorities (Fig. 3a), partially related to the distribution of human land-uses across PNG and the lack of ecological connections between planning units. The ‘connectivity’ land-focused scenario includes one-way riverine connections from upstream to downstream catchments, which shifted terrestrial priorities to upstream catchments with lower erosion, where maintaining vegetation reduces runoff to downstream catchments (Fig. 3b,c). This was particularly noticeable in western mainland New Guinea where priorities’ selection frequency increases dramatically for upstream catchments that would flow into the Gulf of Guinea and Torres Strait (Fig. 2, 3c).

The ‘standard’ marine-focused scenario that ignored connectivity prioritized several high-runoff areas, including the New Britain coast where high coral cover exists (Northeastern Island ecoregion), the Trobirand Islands in the south-east, and coastal areas of Central Range (Fig. 3d). Priorities from the marine-focused ‘connectivity’ scenario shifted away from plumes with high sediment concentrations, such as in the south around the discharge regions for the Central Range ecoregion and the Fly River in the Southern New Guinea ecoregion (Fig. 3e,f). These southern regions with heavy runoff discharge were identified as high conservation priority in the ‘standard scenario’ that did not account for the impacts of upstream land erosion (Fig. 3f).

Including cross-realm connectivity using ‘standard’ approaches shifted some of the land priorities and marine priorities to align such that some adjacent coastal areas and reefs are protected (Fig. 4a). This alignment of connected coastal areas and reefs was maintained when asymmetric land-sea connectivity was included, but priorities moved towards connected upstream catchments (Fig. 4b). For example, terrestrial priorities shifted to capture upstream sub-catchments connected by rivers to coastal reef ecosystems on the mainland such as Northern New Guinea and the Southeast Peninsula (Fig. 4c). Marine priorities in the asymmetric scenario also shifted away from areas of higher runoff (Fig. 4c). For example, inshore marine priorities in the Southeast Peninsula near Popondetta and Alotau shifted further offshore to avoid runoff under the asymmetric connectivity scenario (Fig. 4c).

We found ecoregional differences between the size of the final solution and the amount of conservation features in each connected land-sea region (Tables S4–5). The land-focused best solution was smaller than the land-sea scenario for most island ecoregions by an average 18% (Table S4), and larger by an average 13% for most mainland ecoregions (Northern New Guinea, Central Range, Southern New Guinea, Fig. 5, Table S3). Conversely, total accumulated sediment by ecoregion was on average highest on the mainland (Northern New Guinea, Central Range, Southern New Guinea, mean ~680,000 T per subcatchment) and lowest in the island ecoregions (Southeastern Islands, Admiralty Islands, Trobirand Islands mean ≤25,000 T per subcatchment) (Fig. 5, Table S3). The amount of coral reef in coastal areas connected to land subcatchments was on average inversely related to the accumulated sediment by ecoregion, with highest representation in the island ecoregions, and lowest around the mainland where there is high runoff, with the exception of the Southeast Peninsula where there is relatively high coral cover and moderate levels of runoff (Fig. 5). Solutions that included asymmetric connectivity shifted priorities away from river plumes in this south-eastern region. Turtle nesting beaches on smaller islands (e.g. Trobirand Islands, Manus Island) with low runoff and low erosion (Fig. S1) were also prioritized more in the asymmetric conservation solutions than in the single-realm solutions (Fig. 5, Table S4).

We used outputs of the erosion model to validate our prioritization outputs. Accumulated sediment levels for each reserve network were up to 40% higher in standard solutions than in asymmetric solutions (Fig. 5, Table S5). Although the conservation network was 3% larger overall for the cross-realm asymmetric scenario than for standard scenario (9418 planning units), the total amount of erosion was more than 15% lower ($>3.5e^9$ tonnes) in the asymmetric scenario (Table S5). The lowest erosion levels across the whole network were found in the land-focused scenario ($2.5e^9$ tonnes). Similar ratios were found for local concentrations of sediment in catchments (Table S4).

4. Discussion

Making management or conservation decisions for ecologically connected land-sea systems is inherently challenging, especially in the face of increasing pressure from a growing population, land development, and effects of climate change. We perform an integrated land-sea planning prioritization that incorporates ecological connections to prioritize areas simultaneously across realms, whilst accounting for multiple human pressures. Our analysis demonstrates how incorporating asymmetric land-sea connectivity shifts both terrestrial and marine priorities, emphasizing the importance of accounting for these connections when planning. Furthermore, by considering multiple pressures acting upon the environment both now and into the future and explicitly targeting climate refugia we ensure that resulting conservation plans are more resilient in the long term. Our national-scale prioritization framework is useful for agencies and managers looking to implement actions given multiple objectives, including watershed management and biodiversity protection, and ensures actions are efficient and effective across the land and sea.

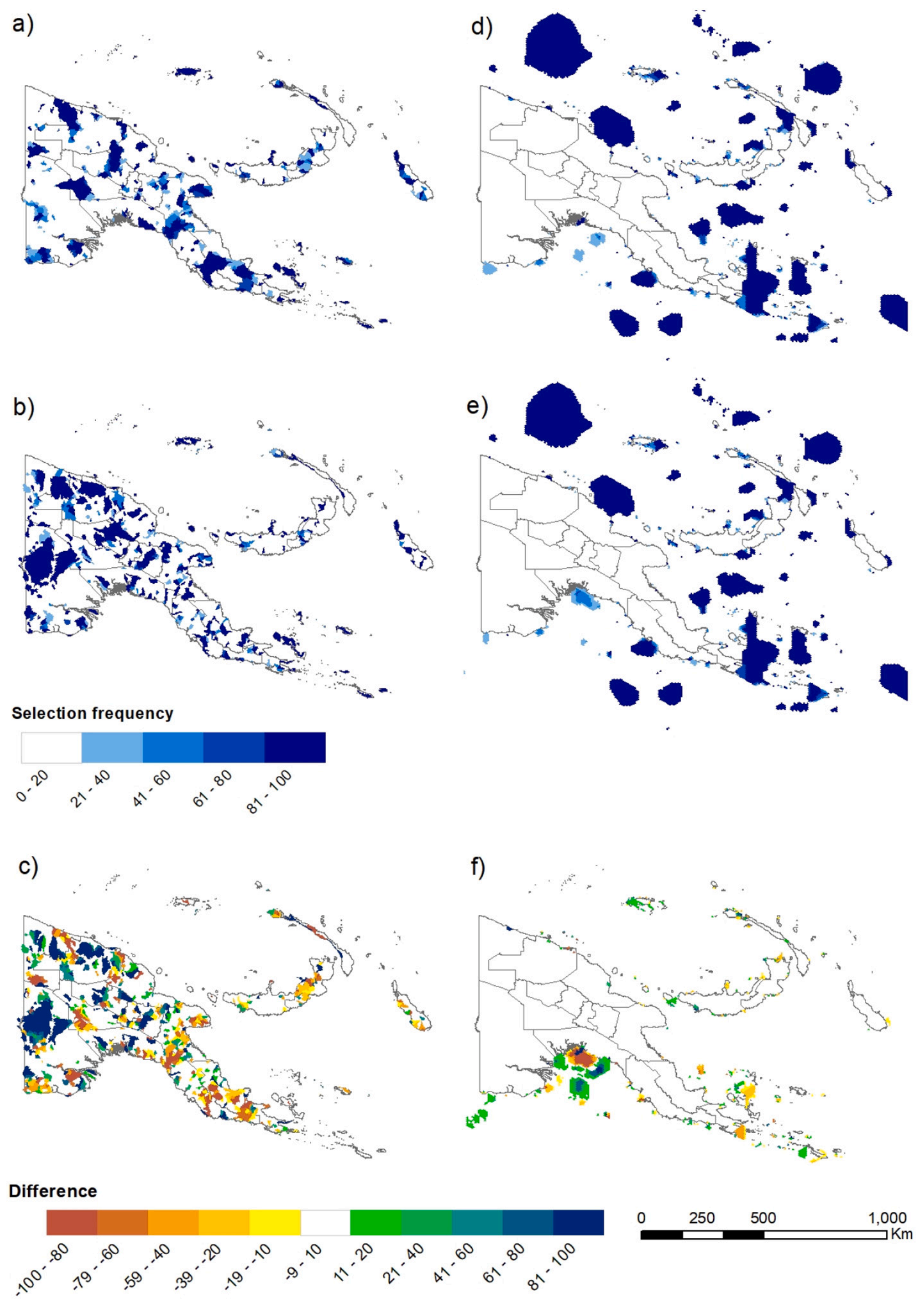

Fig. 3. Land or marine priorities based on: a) Standard land approach; b) Connectivity approach (incorporating riverine connectivity based on runoff model); and c) Difference (connectivity priority value minus standard approach). Marine priorities based on: d) Standard approach; e) Connectivity approach (incorporating land runoff by avoiding plumes); and f) Difference (connectivity minus standard), (where red is a higher conservation priority for standard connectivity, and blue is higher priority for asymmetric connectivity). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Important trade-offs were identified in our comparative analysis of scenarios between accounting for connectivity, costs, and risks to connected downstream marine ecosystems (Fig. 6, Table S5). Ignoring ecological connections between land and sea resulted in erosion levels at the country scale that were 15% higher than if connections were considered. Ecological consequences for downstream marine ecosystems from pollutants in rivers include coral reef mortality, ecosystem degradation and marine turbidity (Fabricius, 2005). In regions with high levels of sediment and/or pollutant runoff, these impacts have already been seen (e.g., the Great Barrier Reef Australia, Fabricius, 2005). Although the land-focused conservation network had lower erosion levels overall, resulting in lower total levels of accumulated sediments in rivers, ecological connections were missing between the land and sea. Because of this, connected land and marine priorities observed in southern areas with higher runoff - such as the Southeast Peninsula of mainland PNG in the asymmetric scenario, linking mangroves, coral reefs and forests - were missing from the land-focused scenarios. The lack of marine priorities in this area means that human activities in the ocean will continue to impact these coastal ecosystems, and land conservation will not improve outcomes for biodiversity downstream. A more efficient connected reserve system prioritizes both downstream and upstream areas simultaneously to avoid threats driven by land and marine activities, as occurs in the asymmetric scenario, thus ensuring maximum effectiveness of conservation efforts. Our framework makes it possible for planners to evaluate such trade-offs in potential management and opportunity costs of conservation versus ecological benefits (Fig. 6, Table S5).

The local and global objectives considered here are defined by single-realm conservation goals, such as forest protection or turtle conservation, or the local impacts of global drivers such as climate change. Cross-realm objectives arise from the relative dependency of local livelihoods on forests and inshore reef environments, and associated importance of connections between the land and sea. The stronger the dependency is on both land and sea resources, the more critical it is to include

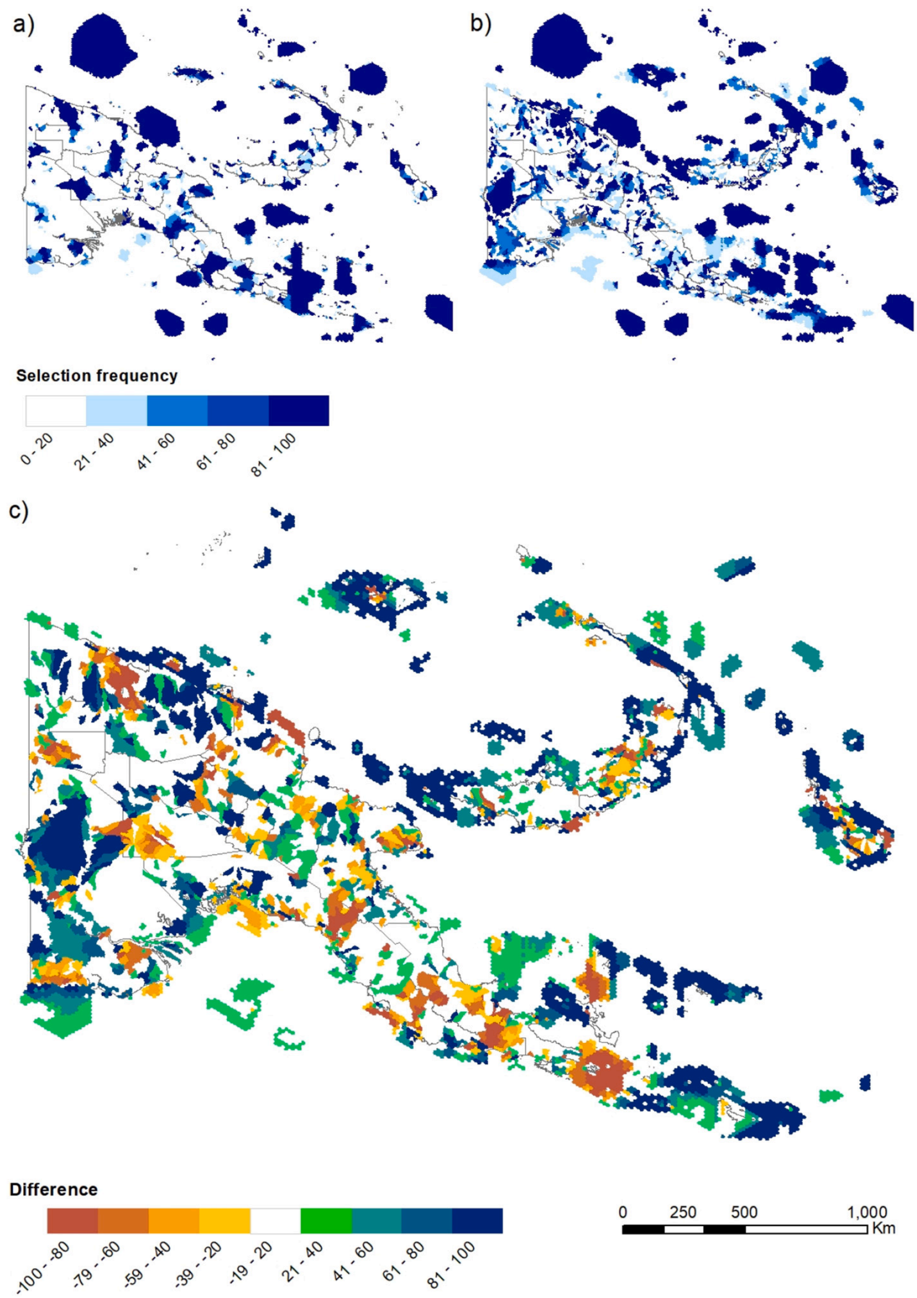

Fig. 4. Land-sea priorities based on: a) standard connectivity; b) incorporating asymmetric land-sea connectivity; and c) difference between asymmetric and standard (where red is higher conservation priority for standard, and blue is higher conservation priority for asymmetric connectivity). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

connectivity in decision-making. For regions like PNG, where local livelihoods are driven by resource availability on the land as well as from coastal reef systems, maintaining high quality connected ecological ecosystems is crucial. In this PNG context, cross-realm conservation was identified as a critical research gap stemming from outcomes of previously developed single-realm plans for land (Lipsett-Moore et al. 2010) and the ocean (Government of Papua New Guinea, 2015). Specifically, the national marine protected area plan conducted in 2014 identified a number of coastal areas for protection that were recognized by local planners as risky due to the chance of inundation or runoff from the land (Government of Papua New Guinea, 2015). Although these single-realm plans may be highly efficient at meeting conservation targets for land or sea biodiversity, they are inefficient when biophysical connections between land-use and coastal ecosystems are considered. This raises issues not only for the effectiveness of conservation measures currently in place, but also economic efficiency of conservation planning. Consideration of cross-realm interactions and objectives prior to investment into initial single-realm plans could have saved considerable time and money, in addition to providing more effective connected conservation plans for land and sea regions.

Equitable conservation action requires consideration of not only impacts of land-use on connected ecosystems, but also divergent socio-economic values and needs of people who rely differently on land and marine resources (Halpern et al., 2013; Turner, 2000). In PNG, the majority of land is under customary tenure (Anderson, 2006), and local community dependency on land and marine ecosystems for livelihoods and resources is high. The average size of the asymmetric conservation networks was slightly larger than those that ignored connectivity, which

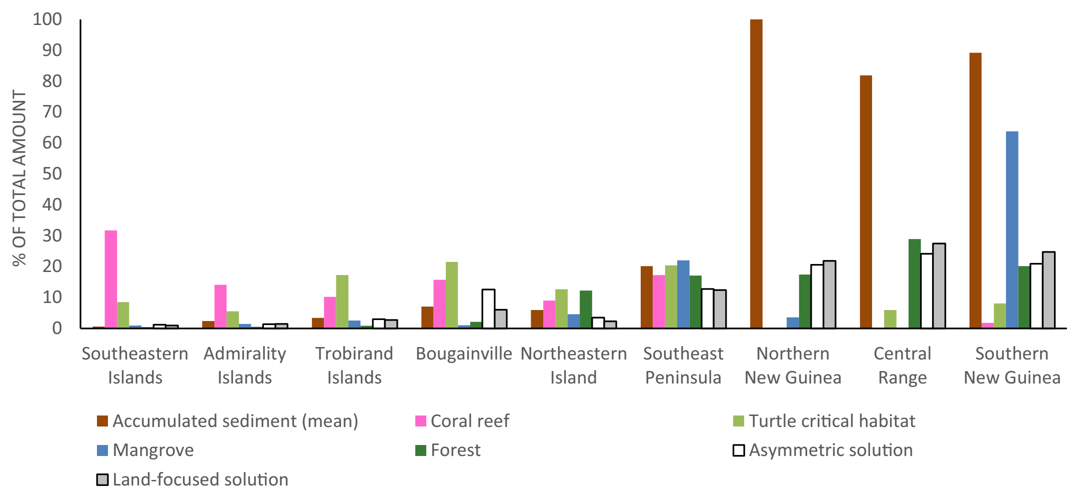

Fig. 5. Amount of coral reef, turtle nesting beaches, mangroves, forest, and accumulated sediment in each ecoregion proportional to the whole country total (as a percentage), with proportional number of planning units selected in the asymmetric land-sea solution and no connectivity (standard) land solution for each ecoregion.

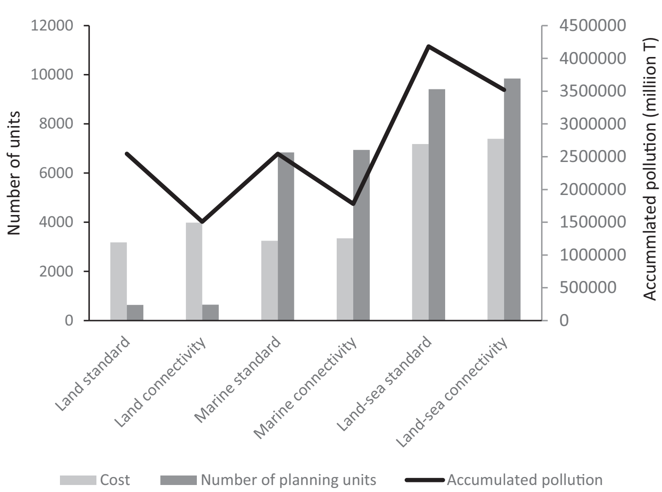

Fig. 6. Trade-offs between costs and number of planning units in each scenario (bars, primary y-axis), and accumulated sediment contained within each final reserve network (black line, secondary y-axis).

may result in slightly higher opportunity costs to local landholders, but important ecological gains could be achieved for downstream marine ecosystems and species by linking priority conservation areas across realms that benefit people dependent on marine resources. For example, considering ecological connectivity would ensure coral reefs that are relatively unaffected by runoff were protected, thus promoting reef resilience and resulting in fish biomass gains (Delevaux et al., 2018; Strain et al., 2019). The question of valuing customary land is of considerable importance in implementing conservation action at local scales. Including information on local land and marine tenure as a cost in our prioritization could improve local uptake and implementation of conservation actions, but most tenure boundaries are not legally mapped across PNG. Furthermore, the size of sub-catchment terrestrial planning units (average 14,400 ha) and marine hexagon planning units (5000 ha) generally vastly exceed the land/sea tenure area of indigenous Papua New Guineans. Establishing protected areas covering prioritized units would therefore require cooperation and consent of multiple landowning groups. Creating the actual protected areas that fully protect the areas prioritized may not be socially feasible, and the larger the number of clans with tenure, the more costly it will be to undertake the consultation to both gain consent and get consensus on rules. We endeavored to meet some of these challenges through ongoing stakeholder engagement and consultation throughout the conservation planning process, and after outputs had been created (see Adams et al., 2016). Work continues at regional scales across PNG towards implementing these plans to ensure conservation meets the needs of local landowners as well as meeting biodiversity objectives.

Consideration of cross-realm ecological and biophysical connections is increasingly recognized in policy to improve water quality, meet global commitments to biodiversity conservation and maximize the success of spatial protection (e.g., Borja et al., 2016). The framework developed here can help nations meet these commitments. For some problems, however, the downstream impacts of land-use may be negligible relative to other concerns, particularly where nearshore marine regions are not within the impact radius of rivers, or where watersheds are relatively pristine with little deforestation, agriculture or populated communities, or in nutrient rich ecosystems (Fredston-Hermann et al., 2016). There are substantial areas throughout the Papua New Guinea mainland and offshore provinces where heavy deforestation has occurred, and where consideration of land-based threats is critical for marine conservation, but many areas of the island provinces have comparatively low erosion levels due to their low-lying geomorphology and size (Table S4), suggesting sediment runoff may not pose a direct threat. Despite this, localized impacts of open-cut mining on reefs have been observed in island regions of PNG (e.g., in Misima Island, Fallon et al., 2002), highlighting the need for connected land-sea planning. Furthermore, consideration of the ecological connections between coastal land and sea systems in conservation planning, such as those between mangroves and reefs, is still crucial to ensure resilience to other disturbances including climate change (Mumby and Hastings, 2008).

A major challenge to integrated land-sea planning is identifying the relationship between actions undertaken on land, and their effects on the marine environment. For tropical reef ecosystems, this relationship is primarily defined by the effects of terrestrial sediment and nutrient run-off on the condition and cover of coral reef habitats and seagrass beds. We used a relatively simple plume model and threshold approach to define and avoid coastal regions with high runoff that could potentially be degraded from high turbidity, sedimentation and nutrients. More rigorous and quantitative methods for linking reef ecosystems to runoff could be used if data were available, such as spatially explicit hydrodynamic modelling of sediment distribution, and accounting for currents and local bathymetry in plume modelling. Alternatively, in situ data on the condition of coastal ecosystems in the prioritization could be included if that were available. Mechanistic models for data-poor regions have also been used to predict the condition of reef ecosystems given different levels of runoff (Tulloch et al., 2016; Wenger et al., 2020). Such methods could be readily incorporated into our framework, as could seascape connectivity approaches that quantify the value of mangroves and coral reefs (Olds et al., 2016). Incorporating such information might shift priorities towards connected mangrove/reef ecosystems, such as in Southern New Guinea, given that high mangrove cover can mitigate the impacts of sediment runoff (Duke and Wolanski, 2000).

Our modelling framework is a useful tool for regions with fewer resources or limited in situ data such as sediment loads that are requirements for more complex modelling. We demonstrate how existing planning products (such as hydroBASINS) and tools (Marxan using asymmetric connectivity feature) can be used in conjunction with readily available data such as IUCN species range maps and land systems, to facilitate land-sea planning in other planning regions. Although we include a range of local, cross-realm and global objectives, many more conservation objectives that could be included, such as representing freshwater biodiversity, and zoning for land development. Inclusion of such factors requires data covering whole region to prevent biased results, but this is not currently available for PNG.

Fully integrated planning, as shown in our asymmetric cross-realm scenario, results in a plan that covers both biodiversity conservation and watershed management objectives, which may require vastly different actions. Choosing which actions should occur in individual planning units requires deeper analysis of in-situ conditions, including identifying what features are present. For example, large upstream areas of Southern New Guinea were prioritized in our asymmetric scenario. This region has high river flow feeding into the Torres Strait, and contains very few priority land conservation features other than mangroves. The prioritization of this region is thus largely for watershed protection, compared to other regions such as provinces in the Admiralty and Northeastern Islands which were prioritized largely for biodiversity protection (e.g., due to high coral coverage, Fig. 5). The decision-making framework presented here provides a substantial advance in our ability to plan for multiple objectives across the land and in the ocean, but further support and interpretation of results is needed to ensure effective implementation of conservation or management actions.

CRediT authorship contribution statement

Vivitskaia J.D. Tulloch: Conceptualization, Methodology, Software, Data curation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition. **Scott Atkinson:** Software, Data curation, Formal analysis, Writing - review & editing. **Hugh P. Possingham:** Conceptualization, Methodology, Funding acquisition, Resources, Supervision. **Nate Peterson:** Resources, Visualization, Writing - review & editing. **Simon Linke:** Resources, Methodology, Writing - review & editing. **James R. Allan:** Validation, Writing - review & editing. **Alu Kaiye:** Data curation, Validation. **Malcolm Keako:** Resources, Validation. **James Sabi:** Resources, Validation. **Bernard Suruman:** Resources, Validation. **Vanessa M. Adams:** Conceptualization, Methodology, Writing - review & editing, Project administration, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.108954.

References

Adams, V.M., Álvarez-Romero, J.G., Carwardine, J., Cattarino, L., Hermoso, V., Kennard, M.J., Linke, S., Pressey, R.L., Stoeckl, N., 2014. Planning across freshwater and terrestrial realms: cobenefits and tradeoffs between conservation actions. Conserv. Lett. 7, 425–440.

Adams, V.M., Tulloch, V.J., Possingham, H.P., 2016. Land-Sea Conservation Assessment for Papua New Guinea: a Report on the Work Undertaken to Fulfil the Terms of the Project Review and Integration of the Terrestrial and Marine Program of Works on Protected Areas. University of Queensland, Australia, and Conservation and Environment Protection Authority, Papua New Guinea.

Allan, J., Levin, N., Jones, K., Abdullah, S., Hongoh, J., Hermoso, V., Kark, S., 2019. Navigating the complexities of coordinated conservation along the river Nile. Sci. Adv. **5**, eaau7668.

Álvarez-Romero, J.G., Pressey, R.L., Ban, N.C., Vance-Borland, K., Willer, C., Klein, C.J., Gaines, S.D., 2011. Integrated land-sea conservation planning: the missing links. Annu. Rev. Ecol. Evol. Syst. 42, 381–409.

Álvarez-Romero, J.G., Adams, V.M., Pressey, R.L., Douglas, M., Dale, A.P., Augé, A.A., Ball, D., Childs, J., Digby, M., Dobbs, R., Gobius, N., Hinchley, D., Lancaster, I., Maughan, M., Perdrisat, I., 2015a. Integrated cross-realm planning: A decision-makers' perspective. Biol. Conserv. 191, 799–808.

Álvarez-Romero, J.G., Pressey, R.L., Ban, N.C., Brodie, J., 2015b. Advancing Land-Sea conservation planning: integrating modelling of catchments, land-use change, and river plumes to prioritise catchment management and protection. PLoS One 10, e0145574.

Anderson, T., 2006. Valuation and registration of customary land in Papua New Guinea. In: Survival of the Commons: Mounting Challenges and New Realities," the Eleventh Conference of the International Association for the Study of Common Property (June 19-23 2006).

Arponen, A., Heikkinen, R.K., Thomas, C.D., Moilanen, A., 2005. The value of biodiversity in reserve selection: representation, species weighting, and benefit functions. Conservation Biology 19, 2009–2014.

Ball, I.R., Possingham, H.P., Watts, M.E., 2009a. Marxan and relatives: Software for spatial conservation prioritization. In: Moilanen, A., Wilson, K.A., Possingham, H.P. (Eds.), Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press, Oxford, UK, pp. 260–268.

Ball, I.R., Watts, M.E., Possingham, H.P., 2009b. Marxan and relatives: software for spatial conservation prioritisation. In: Moilanen, A., Wilson, K.A., Possingham, H.P. (Eds.), Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press, New York City, pp. 185–195.

Ban, N.C., Klein, C.J., 2009. Spatial socioeconomic data as a cost in systematic marine conservation planning. Conserv. Lett. 2, 206–215.

Beger, M., Grantham, H.S., Pressey, R.L., Wilson, K.A., Peterson, E.L., Dorfman, D., Mumby, P.J., Lourival, R., Brumbaugh, D.R., Possingham, H.P., 2010a. Conservation planning for connectivity across marine, freshwater, and terrestrial realms. Biol. Conserv. 143, 565–575.

Beger, M., Linke, S., Watts, M., Game, E., Treml, E., Ball, I., Possingham, H.P., 2010b. Incorporating asymmetric connectivity into spatial decision making for conservation. Conserv. Lett. 3, 359–368.

Beger, M., McGowan, J., Treml, E.A., Green, A.L., White, A.T., Wolff, N.H., Klein, C.J., Mumby, P.J., Possingham, H.P., 2015. Integrating regional conservation priorities for multiple objectives into national policy. Nat. Commun. 6, 8208.

Bertzky, B., Corrigan, C., Kemsey, J., Kenney, S., Ravilious, C., Besançon, C., Burgess, N., 2012. Protected Planet Report 2012: Tracking Progress towards Global Targets for Protected Areas. IUCN, Gland, Switzerland and UNEP-WCMC, Cambridge, UK.

Borja, A., Elliott, M., Andersen, J.H., Berg, T., Carstensen, J., Halpern, B.S., Heiskanen, A.-S., Korpinen, S., Lowndes, J.S.S., Martin, G., 2016. Overview of integrative assessment of marine systems: the ecosystem approach in practice. Front. Mar. Sci. 3, 20.

Brown, C.J., Jupiter, S.D., Albert, S., Anthony, K.R.N., Hamilton, R.J., Fredston-Hermann, A., Halpern, B.S., Lin, H.-Y., Maina, J., Mangubhai, S., Mumby, P.J., Possingham, H.P., Saunders, M.I., Tulloch, V.J.D., Wenger, A., Klein, C.J., 2019. A guide to modelling priorities for managing land-based impacts on coastal ecosystems. J. Appl. Ecol. 56, 1106–1116.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A.,

Tierney, M., Tyrrell, T.D., Vie, J.C., Watson, R., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168.
Carwardine, J., Wilson, K.A., Watts, M., Etter, A., Klein, C.J., Possingham, H.P., 2008. Avoiding costly conservation mistakes: the importance of defining actions and costs in spatial priority setting. PLoS One 3, e2586.
Carwardine, J., Klein, C.J., Wilson, K.A., Pressey, R.L., Possingham, H.P., 2009. Hitting the target and missing the point: target-based conservation planning in context. Conserv. Lett. 2, 4–11.
Cattarino, L., Hermoso, V., Carwardine, J., Kennard, M.J., Linke, S., 2015. Multi-action planning for threat management: A novel approach for the spatial prioritization of conservation actions. PLoS One 10, e0128027.
Cattarino, L., Hermoso, V., Carwardine, J., Adams, V.M., Kennard, M.J., Linke, S., 2018. Information uncertainty influences conservation outcomes when prioritizing multi-action management efforts. J. Appl. Ecol. 55, 2171–2180.
Convention on Biological Diversity, 2010. COP 10 decision X/2: strategic plan for biodiversity 2011–2020. In: 10th Meeting of the Conference of the Parties to the Convention on Biological Diversity, Nagoya, Japan, 18 to 29 October 2010.
Daigle, R.M., Metaxas, A., Balbar, A.C., McGowan, J., Treml, E.A., Kuempel, C.D., Possingham, H.P., Beger, M., 2020. Operationalizing ecological connectivity in spatial conservation planning with Marxan connect. Methods Ecol. Evol. 11, 570–579.
Delevaux, J., Jupiter, S., Stamoulis, K., Bremer, L., Wenger, A., Dacks, R., Garrod, P., Falinski, K., Ticktin, T., 2018. Scenario planning with linked land-sea models inform where forest conservation actions will promote coral reef resilience. Sci. Rep. 8, 1–21.
Duke, N.C., Wolanski, E., 2000. Muddy coastal waters and depleted mangrove coastlines—Depleted seagrass and coral reefs. Reefs. CRC Press, Oceanographic Processes of Coral, pp. 97–112.
Eslinger, D., VanderWilt, M., Dempsey, E., Carter, J., Wilson, B., 2005. The nonpoint-source pollution and erosion Comparison Tool. Coastal GeoTools'05 32.
Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar. Pollut. Bull. 50, 125–146.
Fallon, S.J., White, J.C., McCulloch, M.T., 2002. Porites corals as recorders of mining and environmental impacts: Misima Island, Papua New Guinea. Geochim. Cosmochim. Acta 66, 45–62.
Fredston-Hermann, A., Brown, C.J., Albert, S., Klein, C.J., Mangubhai, S., Nelson, J.L., Teneva, L., Wenger, A., Gaines, S.D., Halpern, B.S., 2016. Where does river runoff matter for coastal marine conservation? Front. Mar. Sci. 3, 273.
Gissi, E., McGowan, J., Venier, C., Carlo, D.D., Musco, F., Menegon, S., Mackelworth, P., Agardy, T., Possingham, H., 2018. Addressing transboundary conservation challenges through marine spatial prioritization. Conserv. Biol. 32, 1107–1117.
Government of Papua New Guinea, 2015. National Marine Conservation Assessment for Papua New Guinea. Port Moresby, Conservation and Environment Protection Authority, p. 51.
Green, A., Kertesz, M., Peterson, N., Retif, S., Skewes, T., Dunstan, P., McGowan, J., Tulloch, V., Kahn, B., Kertesz, M., 2014. A regionalisation of Papua New Guinea's marine environment. In: Technical Report for PNG DEC.
Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A Global Map of Human Impact on Marine Ecosystems. Science 319, 948–952.
Halpern, B.S., Ebert, C.M., Kappel, C.V., Madin, E.M.P., Micheli, F., Perry, M., Selkoe, K. A., Walbridge, S., 2009. Global priority areas for incorporating land–sea connections in marine conservation. Conserv. Lett. 2, 189–196.
Halpern, B.S., Klein, C.J., Brown, C.J., Beger, M., Grantham, H.S., Mangubhai, S., Ruckelshaus, M., Tulloch, V.J., Watts, M., White, C., Possingham, H.P., 2013. Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation. Proc. Natl. Acad. Sci. 110, 6229–6234.
Hermoso, V., Kennard, M.J., Linke, S., 2012. Integrating multidirectional connectivity requirements in systematic conservation planning for freshwater systems. Divers. Distrib. 18, 448–458.
Jones, K.R., Maina, J.M., Kark, S., McClanahan, T.R., Klein, C.J., Beger, M., 2018. Incorporating feasibility and collaboration into large-scale planning for regional recovery of coral reef fisheries. Mar. Ecol. Prog. Ser. 604, 211–222.
Klein, C.J., Ban, N.C., Halpern, B.S., Beger, M., Game, E.T., Grantham, H.S., Green, A., Klein, T.J., Kininmonth, S., Treml, E., Wilson, K., Possingham, H.P., 2010. Prioritizing land and sea conservation investments to protect coral reefs. PLoS One 5, e12431.
Klein, C.J., Jupiter, S.D., Watts, M., Possingham, H.P., 2014. Evaluating the influence of candidate terrestrial protected areas on coral reef condition in Fiji. Mar. Policy 44, 360–365.
Linke, S., Pressey, R.L., Bailey, R.C., Norris, R.H., 2007. Management options for river conservation planning: condition and conservation re-visited. Freshw. Biol. 52, 918–938.
Linke, S., Kennard, M.J., Hermoso, V., Olden, J.D., Stein, J., Pusey, B.J., 2012. Merging connectivity rules and large-scale condition assessment improves conservation adequacy in river systems. J. Appl. Ecol. 49, 1036–1045.
Linke, S., Lehner, B., Dallaire, C.O., Ariwi, J., Grill, G., Anand, M., Beames, P., Burchard-Levine, V., Maxwell, S., Moidu, H., 2019. Global hydro-environmental sub-basin and river reach characteristics at high spatial resolution. Scientific Data 6, 1–15.
Lipsett-Moore, G., Game, E., Peterson, N., Saxon, E., Sheppard, S., Allison, A., Michael, J., Singadan, R., Sabi, J., Kula, G., 2010. Interim national terrestrial conservation assessment for Papua New Guinea: protecting biodiversity in a changing climate. Report no. 1/2010. Papua New Guinea Department of Environment and Conservation, The Nature Conservancy, and United Nations Development Programme, Brisbane.
Magris, R.A., Treml, E.A., Pressey, R.L., Weeks, R., 2016. Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography 39, 649–664.
Makino, A., Beger, M., Klein, C.J., Jupiter, S.D., Possingham, H.P., 2013. Integrated planning for land–sea ecosystem connectivity to protect coral reefs. Biol. Conserv. 165, 35–42.
Merritt, W.S., Letcher, R.A., Jakeman, A.J., 2003. A review of erosion and sediment transport models. Environ. Model. Softw. 18, 761–799.
Mittermeier, R.A., Myers, N., Thomsen, J.B., Da Fonseca, G.A.B., Olivieri, S., 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conserv. Biol. 12, 516–520.
Mumby, P.J., 2006. Connectivity of reef fish between mangroves and coral reefs: algorithms for the design of marine reserves at seascape scales. Biol. Conserv. 128, 215–222.
Mumby, P.J., Hastings, A., 2008. The impact of ecosystem connectivity on coral reef resilience. J. Appl. Ecol. 45, 854–862.
Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H., Rouget, M., 2006. Integrating economic costs into conservation planning. Trends Ecol. Evol. 21, 681–687.
NSO, 2011. 2011 National Population and Housing Census of Papua New Guinea -Final Figures. National Statistical Office of Papua New Guinea. Port Moresby, PNG.
Olds, A.D., Connolly, R.M., Pitt, K.A., Pittman, S.J., Maxwell, P.S., Huijbers, C.M., Moore, B.R., Albert, S., Rissik, D., Babcock, R.C., 2016. Quantifying the conservation value of seascape connectivity: a global synthesis. Glob. Ecol. Biogeogr. 25, 3–15.
Possingham, H.P., Ball, I.R., Andelman, S., 2000. Mathematical methods for identifying representative reserve networks. In: Ferson, S., Burgman, M.A. (Eds.), Quantitative Methods for Conservation Biology. Springer-Verlag, pp. 291–309.
Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S., Pulliam, H.R., 2001. Making smart conservation decisions. Conservation Biology: Research Priorities for the Next Decade 23, 225–244.
Randall, J.E., 1998. Zoogeography of shore fishes of the indo-Pacific region. Zool. Stud. 37, 227–268.
Rodríguez-Guzmán, V., Gilbes-Santaella, F., 2009. Using MODIS 250 m imagery to estimate total suspended sediment in a tropical open bay. International Journal of *SYSTEMS APPLICATIONS*, engineering & Development 3, 36–44.
Shearman, P., Bryan, J., 2011. A bioregional analysis of the distribution of rainforest cover, deforestation and degradation in Papua New Guinea. Austral Ecology 36, 9–24.
Stein, J., 2018. An enhanced Pfafstetter catchment reference system. Water Resour. Res. 54, 9951–9963.
Stoms, D.M., Davis, F.W., Andelman, S.J., Carr, M.H., Gaines, S.D., Halpern, B.S., Hoenicke, R., Leibowitz, S.G., Leydecker, A., Madin, E.M.P., Tallis, H., Warner, R.R., 2005. Integrated coastal reserve planning: making the land-sea connection. Front. Ecol. Environ. 3, 429–436.
Strain, E.M., Edgar, G.J., Ceccarelli, D., Stuart-Smith, R.D., Hosack, G.R., Thomson, R.J., 2019. A global assessment of the direct and indirect benefits of marine protected areas for coral reef conservation. Divers. Distrib. 25, 9–20.
Tallis, H., Ferdana, Z., Gray, E., 2008. Linking terrestrial and marine conservation planning and threats analysis. Conserv. Biol. 22, 120–130.
Tsang, Y.-P., Tingley III, R.W., Hsiao, J., Infante, D.M., 2019. Identifying high value areas for conservation: accounting for connections among terrestrial, freshwater, and marine habitats in a tropical island system. J. Nat. Conserv. 50, 125711.
Tulloch, A.I.T., Tulloch, V.J.D., Evans, M.C., Mills, M., 2014. The value of using feasibility models in systematic conservation planning to predict landholder management uptake. Conserv. Biol. 28, 1462–1473.
Tulloch, V.J., Brown, C.J., Possingham, H.P., Jupiter, S.D., Maina, J.M., Klein, C., 2016. Improving conservation outcomes for coral reefs affected by future oil palm development in Papua New Guinea. Biol. Conserv. 203, 43–54.
Tulloch, V.J., Klein, C.J., Jupiter, S.D., Tulloch, A.I.T., Roelfsema, C., Possingham, H.P., 2017. Trade-offs between data resolution, accuracy, and cost when choosing information to plan reserves for coral reef ecosystems. J. Environ. Manag. 188, 108–119.
Turner, R.K., 2000. Integrating natural and socio-economic science in coastal management. J. Mar. Syst. 25, 447–460.
USDA, 1986. Technical Release: Urban hydrology for small watersheds. In: Natural Resources Conservation Service, Conservation Engineering Division. ed. USDA. United States Department of Agriculture, Washington, DC, p. 164.
Wenger, A.S., Harris, D., Weber, S., Vaghi, F., Nand, Y., Naisilisili, W., Hughes, A., Delevaux, J., Klein, C.J., Watson, J., Mumby, P.J., 2020. Best-practice forestry management delivers diminishing returns for coral reefs with increased land-clearing. Journal of Applied Ecology 57 (12), 2381–2392.
White, J.W., Schroeger, J., Drake, P.T., Edwards, C.A., 2014. The value of larval connectivity information in the static optimization of marine reserve design. Conserv. Lett. 7, 533–544.
Wolff, N.H., Da Silva, E.T., Devlin, M., Anthony, K.R., Lewis, S., Tonin, H., Brinkman, R., Mumby, P.J., 2018. Contribution of individual rivers to great barrier reef nitrogen exposure with implications for management prioritization. Mar. Pollut. Bull. 133, 30–43.