Multi-scale estimation of the effects of pressures and drivers on mangrove forest loss globally


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ABSTRACT

Human activities that threaten ecosystems often vary across small spatial scales, though they can be driven by large-scale factors like national governance. Here, we use two decades of data on global mangrove deforestation to assess whether landscape-scale indirect pressures – cumulative impacts, population density, mangrove forest fragmentation, the global human footprint – and management responses (protected areas) are related to rates of mangrove loss, and whether the impacts of these activities vary by nation. By integrating rates of loss at different spatial scales into a Bayesian hierarchical model, we also assess whether national-scale patterns in mangrove loss are predicted by national regulatory quality. Globally, less fragmented forests had lower rates of mangrove loss. We observed variability among nations in the effect of pressures and management responses on mangrove loss. National regulatory quality mediated how pressures and management interact to influence mangrove loss. Protected areas had a greater benefit for slowing mangrove loss rates in countries with low, rather than high, regulatory quality, ostensibly because countries with higher regulatory quality have greater protection of mangroves outside of protected areas. High population densities were also associated with greater mangrove loss, but only in nations with low regulatory quality. We suggest that efforts to protect mangrove forests will benefit from developing solutions that consider national context and address differences in the effect of pressures and cumulative impacts. Our model can also be applied to other globally threatened ecosystems to understand how variation in local context can affect national-scale conservation outcomes.

1. Introduction

Mangrove forests are one of the world's most threatened ecosystems (Fries, 2016). Mangrove loss is caused by a range of activities such as aquaculture, agriculture, urban development and harvesting of forest products. (Alongi, 2002; Giri et al., 2011; Richards and Fries, 2016; Fries et al., 2019). Beyond direct land conversion, multiple indirect pressures such as climate change (Gilman et al., 2008; Sippo et al., 2018) and associated sea-level rise (Lovelock et al., 2015), altered hydrological regimes, and increased pollution (Alongi, 2002, 2012), further compound the stress placed on mangrove forests.

Mangrove forest conservation is increasingly attracting international interest, in recognition of the essential and valuable services mangroves provide, including climate regulation through carbon storage, coastal protection, biodiversity conservation and contribution to fisheries production (Atwood et al., 2017; Hamilton and Fries, 2018; Hochard et al., 2019; Sievers et al., 2019). Mangrove ecosystems and their associated services contribute to the delivery of global targets including the United Nations Sustainable Development Goals (SDGs), Aichi Biodiversity Targets, Bonn Challenge, and the Paris Agreement on Climate Change (Ramsar Convention on Wetlands, 2018). Consequently, new global-scale attempts to restore and protect mangroves are now supplementing pre-existing efforts that generally have a more local or regional focus. For instance, the Global Mangrove Alliance, an alliance between multiple major global conservation organisations, has set ambitious targets for increasing global mangrove extent (The Global Mangrove Alliance, 2017). Such international initiatives are important for attracting global funding for conservation in low- or lower-middle-
income economies; however a ‘one-size-fits-all’ approach to conservation across different nations often proves ineffective (Mahajan et al., 2019).

Mangrove conservation must consider diverse socio-economic, cultural and political challenges that vary across regions and nations (Frieds et al., 2016). For instance, the effectiveness of protected areas (PAs) at halting mangrove deforestation is known to vary across Central and South America (López-Angarita et al., 2018). In nations with poor management capacity, PAs alone are often insufficient to conserve biodiversity (Amano et al., 2017; Gill et al., 2017). Furthermore, the effects of pressures on rates of mangrove loss may depend on national context, where the same threatening process may have very different impacts in different nations, confounding global actions to prevent ecosystem decline. Variation in the effects of pressures, and of PAs, creates a challenge for international initiatives because they must set global funding priorities while working within the constraint that conservation actions need to be locally-adapted to be effective (Waldron et al., 2013; Brandt et al., 2019).

Recent efforts to map the status and trends of mangrove forests globally (e.g. Hamilton and Casey, 2016; Bunting et al., 2018) have been crucial for identifying and quantifying the activities (e.g. direct land conversion for aquaculture, coastal development, palm oil plantations) affecting mangrove forest extent (Richards and Frieds, 2016; Thomas et al., 2017). Remote sensing studies quantify and highlight where mangrove habitats have already been lost, however there remains a scarcity of information on where future changes are likely to occur based on indirect pressures. It is unclear whether hotspots of pressures are related to areas of high mangrove deforestation, or whether the impacts of pressures vary in response to specific national-scale drivers, including indicators of governance. Spatially quantifying how these pressures affect the state of mangroves can guide conservation efforts and contribute to tailoring conservation interventions to address these threats.

Here we aim to quantify how trends of mangrove forest loss are related to pressures and drivers at multiple spatial scales based on hypothesised relationships. To analyse multi-scale patterns in mangrove deforestation we use recent, high resolution spatio-temporal mapping of global mangrove forest cover between 1996 and 2016 (Bunting et al., 2018) and develop Bayesian hierarchical models within a Drivers, Pressures, State changes, Impact, and Response (DPSIR) framework (Elliott et al., 2007). We use this approach to capture the landscape-scale differences in pressures and state changes that are commonly used as indicators in conservation prioritisation. We further investigate the possibility that the effects of pressures on state changes vary with large scale drivers, which are related to (but removed from), replacement land use activities such as aquaculture and agriculture. Here, pressures include a range of anthropogenic threats (Table 1), while state change is defined as mangrove loss. This approach also allows us to assess whether management responses such as the designation of PAs influence mangrove loss. We specifically ask: 1) Do landscape-scale pressures and management responses explain recent trends in mangrove loss, and do these effects vary by nation? 2) Do the landscape-scale effects of pressures and PAs vary systematically with national scale drivers?

2. Methods

DPSIR is a causal framework adapted initially and extended by the European Environment Agency to describe interactions between society and the environment (Elliott et al., 2007). This framework is widely used across ecological research and management to support decision making and can be applied from local to global scales (Tscherning et al., 2012). We used the DPSIR framework to inform a hierarchical analysis that modelled proportional mangrove loss at a landscape-scale as dependent on direct pressures and responses (referred to as management response), which are mediated by national drivers (Fig. 1). We begin with the methods on mangrove state change, because this is the response variable in our DPSIR model and it is important to understand how this variable was measured before we explain drivers, pressures and responses.

2.1. State changes

We used a high-resolution (~30 m × 30 m) global dataset describing mangrove extent in 7 time steps from 1996 to 2016 (Bunting et al., 2018 – available at https://data.unep-wcmc.org/datasets/45). To represent mangrove landscapes, data were spatially aggregated to 20 km × 20 km grid cells (400 km² – henceforth referred to as landscapes), resulting in 8774 individual landscapes. Decline in mangrove extent for the time series was calculated for each landscape between 1996 and 2016 (i.e. a single time-step) by summing the total change in area of all 30 m × 30 m cells within a landscape. Although this dataset includes mangrove reafforestation, we focussed only on estimates of how pressures affect loss so did not include any estimates of mangrove gain from 1996 in our analysis. Landscapes were then converted to a local Universal Transverse Mercator (UTM) and exported as GeoTIFFs. All data processing was done in R (version 3.4.1) using the package raster (Hijmans et al., 2015).

2.2. Drivers

Regulatory quality is a component of the World Governance Indicators that “captures perceptions of the ability of the government to formulate and implement sound policies and regulations that permit and promote private sector development” and includes information on the stringency of environmental regulations (Kauffman et al., 2009). We expected lower mangrove loss in nations with higher regulatory quality as biodiversity aid and conservation funding are positively associated with more regulated nations (Miller et al., 2013). We used national regulatory quality values from 1996 as being most relevant to mangrove losses over the subsequent two decades. We also tested regularity quality in 2016, but values were highly correlated with 1996 (correlation coefficient of 0.87 for 1996 vs 2016) indicating that national values regulatory quality were relatively stable across the time-series. We also tested indices of per capita Gross Domestic Product (GDP) as a national driver because data existed for more nations, however GDP and regulatory quality were highly correlated (r² = 0.70), and similar patterns were found, so no further analyses were carried out using GDP or other economic indicators such as GNI (Table 1).

2.3. Pressures

We included four pressure indicators hypothesised to impact mangroves (Fig. 1, Table 1). First, we hypothesised that mangrove loss would be higher in areas subject to greater human cumulative local and global scale impacts, consistent with the expectation that mangrove loss is often greatest in areas subject to both global climate (e.g. Lovelock et al., 2015; Schuerch et al., 2018; Sippo et al., 2018) and direct human pressures (Thomas et al., 2017). Since mangroves are at the interface of marine and terrestrial systems, we tested how both marine and terrestrial pressures may be contributing to mangrove loss. To do this, we used an indicator representing the cumulative effects of multiple stressors on marine systems (Halpern et al., 2008), and the global human footprint to account for terrestrial stressors (Venter et al., 2016). Both of these pressure measures combined impacts from different threats into a single aggregate measure. These include pressures that are predicted to be key drivers of mangrove loss, including climate change, local human pressures like exploitation, and regional pressures like pollution (Alongi, 2002; Chowdhury et al., 2017; Sippo et al., 2018). For cumulative marine threats, only layers relevant to mangrove ecosystems were selected (e.g. nutrient input, commercial activity, non-point organic pollution and sea temperature), based on the risk metrics
Table 1
List of covariates and their description, link to DPSIR framework, and data source used in the Bayesian hierarchical models.

<table>
<thead>
<tr>
<th>Covariate &amp; description</th>
<th>DPSIR step</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>National Regulatory Quality</td>
<td>Drivers</td>
<td>World Governance Indicators</td>
</tr>
<tr>
<td></td>
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<td><a href="http://info.worldbank.org/governance/wgi/">http://info.worldbank.org/governance/wgi/</a></td>
</tr>
<tr>
<td>Terrestrial Human Footprint</td>
<td>Pressure</td>
<td>Socioeconomic Data and Applications Center: A Data Center in NASA's Earth Observing System Data and Information System</td>
</tr>
<tr>
<td>Cumulative Marine Impacts</td>
<td>Pressure</td>
<td>Knowledge Network for Biocomplexity (KNB) repository</td>
</tr>
<tr>
<td>Fragmentation</td>
<td>Pressure</td>
<td>Fragstats (McGarigal, Cushman, &amp; Ene, 2012)</td>
</tr>
<tr>
<td>Population Density</td>
<td>Pressure</td>
<td>Socioeconomic Data and Applications Center: A Data Center in NASA's Earth Observing System Data and Information System</td>
</tr>
<tr>
<td>Protected Areas</td>
<td>Response</td>
<td>Protected Planet: Discovery the worlds protected areas</td>
</tr>
<tr>
<td></td>
<td></td>
<td><a href="http://www.protectedplanet.net">www.protectedplanet.net</a></td>
</tr>
</tbody>
</table>

Fig. 1. Conceptual model depicting how a state change in global mangrove forest loss is potentially affected by drivers, pressures, and responses at two spatial scales. The arrows indicate that drivers mediate how pressures and responses affect state change. The blue shaded box indicates what is assessed in this model (Note impacts within the DPSIR framework are not directly assessed in this instance). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
to inform the vulnerability of ecosystems in Halpern et al. (2008). Threats with a risk value of ‘0’ were excluded from the final cumulative map (e.g. demersal destructive fishing and pelagic fishing were removed). We did not attempt to partition the effects of individual stressors because the spatial distribution of different pressures strongly covaries, precluding the statistical separation of effects based on spatial gradients alone. Mangrove management requires a landscape-scale approach (Fatyoinbo et al., 2008), hence aggregating measures at the relatively large spatial scale of 20 km × 20 km is an appropriate level of precision for this analysis.

We also included the initial degree of habitat fragmentation in mangrove forest patches as a pressure in our models. We hypothesised that fragmented forests would experience higher rates of loss because fragmentation increases the vulnerability of mangrove forests to extreme weather events, and increases accessibility, facilitating anthropogenic disturbances including clearing, pollution and altered hydrology (Li et al., 2013). Fragmentation was represented by the metric ‘mean patch area’ within each landscape. This metric represents a measure of average patch size and down-weights the influence of small patches (McGarigal et al., 2012). We hypothesised that landscapes with larger mean patch areas in 1996 would be more resilient to loss than landscapes with smaller mean patch sizes, while acknowledging that this metric does not account for all aspects of the configuration of mangrove patches within each landscape. Fragmentation metrics were calculated for each landscape (sensu Bryan-Brown et al., 2020), using the same data used to quantify mangrove state change. Calculations were performed using the Fragstats program (McGarigal et al., 2012).

Finally, we included human population density as a proxy measure of the effect of human activities of mangroves. We consider this proxy indicator to represent several possible direct human pressures on mangroves: harvesting of mangrove wood; clearing for coastal development (Ilman et al., 2016); high traffic use (Greich et al., 2013); and the coastal armouring that prevents mangroves migrating inland in response to sea level rise (Gittman et al., 2015). Human density has also been used as an indicator of coastal armouring in models of future predicted mangrove change (Schuerch et al., 2018), so it is important to assess its ability to predict past change. We hypothesised that mangrove loss would be greater in more densely populated regions (Kumar, 2012).

2.4. Impacts

Impacts are commonly interpreted as the impact of state changes on ecosystems, economies and society. We chose to focus on exploring how mangrove state is related to pressures and drivers at multiple spatial scales. Future studies could expand our analysis to consider the connection between mangrove loss and its impacts.

2.5. Response (management response)

The management response included in the model was all marine, coastal, and terrestrial PAs that were designated or in place before 2008. We used the World Database on Protected Areas (WDPA) (www.protectedplanet.net) and calculated the percentage of the total area that was protected within each landscape. We hypothesised that greater protected area coverage would result in lower rates of mangrove loss (López-Angarita et al., 2018). We acknowledge that mangroves are often protected under a range of other means including under federal and state legislation, indigenous land or under community management. However given the lack of globally available data quantifying this, we did not account for these types of protection in the current study meaning our results likely underestimate the effects of protected areas.

2.6. Data processing

Values for pressures and responses were averaged across the landscape (i.e. 20 km × 20 km) to match the spatial resolution of mangrove loss. In some cases, landscapes did not intersect with any pressure layer (i.e. terrestrial footprint or cumulative impacts on marine ecosystems layers). In these cases, we intersected the features with a search radius of 100 km. This search radius was selected as an appropriate distance to intersect mangrove landscapes that were located inland from the marine cumulative impacts data (e.g. The Gambia River in The Gambia, Western Africa). Mangrove cells that still could not be intersected after applying the radius were excluded from the study (< 1% of cells). All spatial processing was done using ArcGIS 10.3 (ESRI, 2015). A total of 77 nations and 8292 landscapes with existing mangroves had data for all of the covariates. Therefore, the data-set covered 94.5% of the mapped mangrove habitat from Bunting et al. (2018).

2.7. Statistical methods

2.7.1. Overview

We used a multi-scale Bayesian hierarchical modelling approach to estimate and quantify relationships between mangrove loss, and both landscape and national-scale covariates. The regressions between mangrove loss and landscape-scale covariates were fit and simultaneously regressed against national-scale drivers (Gelman and Hill, 2006). Hence, this model essentially fits a cross-scale interaction, allowing us to explore relationships between landscape-level pressures and national-level drivers. Analogous frequentist approaches (such as GLMMs) are not flexible enough to allow testing of complex interactions, which are possible using a hierarchical Bayesian framework. The goal was not to take an exhaustive approach to fitting every single potential predictor variable possible. Instead, we restricted our analyses to globally available datasets that were hypothesised to impact mangrove deforestation. We tested for collinearity between our covariates using Spearman’s rank correlation coefficient. We included all five landscape-level covariates in our final model because the Spearman rank correlation coefficient indicated no collinearity between variables (< 0.5).

2.8. Model of landscape-scale covariates

2.8.1. National estimates and variation in mangrove loss: responses to landscape-scale pressures and management responses

At the landscape-scale, we estimated the state change in mangrove cover from 1996 to 2016 based on covariates that represented pressures and management responses. The model allowed the landscape-scale effects of the covariates to vary by nation. The nation-level effects of covariates were contingent on national drivers.

Our response variable, the log landscape-scale area of mangroves present in 2016, was assumed to be normally distributed with the mean related to landscape-scale covariates.

\[
y_{ij2016} = \log\left(\frac{N_{ij}}{y_{ij1996}}\right) = \beta_{0j} + \beta_{1j}X_{ij1} + \cdots + \beta_{Nj}X_{ijN}
\]

where \(y_{ij1996}\) is the mangrove area in 2016 in landscape \(i\) in nation \(j\). The mean, \(\log(\mu_{ij2016})\), is the mean of the posterior distribution estimating the log mangrove area in 2016, and \(\tau\) is the precision (1/variability) of the normal distribution. We include an offset term in the model, \(\log\left(y_{ij1996}\right)\), which is the log total area of mangroves measured in 1996. Rearranging this equation, the median posterior estimates from the model are the log proportion of mangrove area in 2016 relative to the area in 1996, related to \(N\) landscape-scale covariates, \(X_{ij1} \ldots X_{ijN}\).

\[
\log(\mu_{ij2016}) = \beta_{0j} + \beta_{1j}X_{ij1} + \cdots + \beta_{Nj}X_{ijN}
\]

where \(\beta_{0j}\) are intercepts and \(\beta_{1j} \ldots \beta_{Nj}\) are slopes. We mean centred and standardized the covariates, \(X_{ij1} \ldots X_{ijN}\), so that the intercepts represented the log proportional mangrove loss at national average levels of the covariates. The slope terms quantify the relationships between the landscape-scale...
covariates ($X_{ij1}...X_{ijN}$) and estimated mangrove loss in the $j$th nation. The slopes and intercepts were drawn from a normal prior distribution:

$$\beta_{jk} \sim \mathcal{N}(\Omega_{jk}, P_k)$$

where $P_k$ are the precisions of the normal distributions for $\beta_{jk}$.

### 2.9. Model of national-scale drivers

#### 2.9.1. Systematic variation of landscape-scale effects of pressures and protected areas with national scale drivers

The national-scale drivers model quantifies how landscape-scale relationships between mangrove loss, pressures and management responses vary systematically with national-scale covariates, $Z_j$:

$$\hat{\beta}_j = \Omega_{k0} + \Omega_{k1}Z_j$$

where $\Omega_{k0}$ is the intercept and $\Omega_{k1}$ is the slope that quantifies relationships between landscape-scale regression coefficient estimates and national-scale covariates in the driver model. As the landscape-scale intercepts are estimates of the log national proportional mangrove loss, the nation-level intercepts of the regression of these parameters quantifies the mean global effects of landscape-scale pressures and responses.
2.10. Priors

We used weakly informative gamma prior distributions for the precision terms; \( \tau_i \sim \Gamma(2, 0.5) \), and uninformative multivariate normal prior distributions for the regression relationships at the upper level of the model; \( \Omega_k \sim \text{MVN}(0, 0.001) \). We fit weakly informative priors; \( P_i = \text{pow}(\sigma_i, -2) \), \( \sigma_k \sim \Gamma(1, 1) \) on the intercepts and slopes of the \( \beta \) coefficients to ensure shrinkage towards the global mean and avoid overfitting, while still allowing the likelihood to estimate effects where the data were strongly informative (Simpson et al., 2017). Comparative national estimates of loss based on broad priors are shown in Fig. S1. Parameter shrinkage was important in this model to reduce the risk of falsely detecting nation-level effects due to the large number of parameters estimated.

All models were fit using JAGS called from R statistical software version 3.5.1 (R Development Core Team, 2017) using the packages R2jags (Su and Yajima, 2015). Models were run for 100,000 iterations across 2 chains, thinned by 10, with a burn in of 10,000, leaving 18,000 posterior samples to calculate maximum a posteriori estimates. Model convergence was confirmed with \( R \) values. Model residuals were examined and were normally distributed.

We included all the landscape covariates in our models and evaluated their effect sizes based on one-sided probability levels, such that a probability of 0.5 indicates an ambiguous effect because there is equal probability the effect is either positive or negative. Initially, we compared the mean rate of loss per nation as estimated by the model to the same statistic estimated from the raw data, as a verification step.

3. Results

3.1. Model verification - national estimates and variation in mangrove loss

The model estimated that the greatest mean proportional losses of mangroves per landscape were concentrated in Asia (Bangladesh, Myanmar, India, Pakistan, Vietnam and Sri Lanka), and the Bahamas (Fig. 2). Fiji and New Zealand were estimated to have the lowest proportional mangrove loss between 1996 and 2016. Landscape-scale predictions were highly accurate (\( r^2 = 0.94 \); Fig. S2), and national estimates of mean loss per landscape were largely consistent with the underlying data of Bunting et al. (2018) (\( r^2 = 0.51 \); Fig. S3), though notably the model overestimated mean landscape-scale rates of loss in Bangladesh, Myanmar and India. Estimates were partially sensitive to the choice of priors; however this did not alter estimates for nations with the highest predicted losses (see Fig. S1 for mean and variation in national-level parameter estimates based on uninformative priors). Prior influence had the greatest effect where variation in loss was weakly associated with variation in the covariates.

3.2. Responses to landscape-scale pressures and management responses

Globally, we found several highly probable relationships between proportional mangrove loss and the landscape covariates (Table 2). At a global scale, mean patch area was positively related to the proportion of mangrove area remaining (> 0.99 probability), indicating that nations with larger mangrove patches in 1996 (i.e. less fragmented mangrove forests) experienced lower proportional losses compared to regions with smaller mangrove patches (Table 2, Fig. S4). This effect was consistently positive across all 77 nations, though there was spatial variability in the size of the effects (Fig. 3).

Higher population density was associated with greater rates of mangrove loss at a global scale; however this effect was only moderately probable (0.84 probability – Table 2; Fig. S5). At a national scale, Myanmar, Saudi Arabia and Indonesia had the strongest negative effects from population density when compared with the global mean suggesting that, in these nations, locations with higher population densities are associated with more severe mangrove losses relative to other nations.

Protected areas had an overall positive effect on mangrove area, suggesting that greater protected area coverage is associated with lower mangrove loss at a global scale. However, this relationship was only moderately probable (0.78 probability – Table 2; Fig. S6) and there was considerable national-scale uncertainty in these relationships, though a high probability that greater coverage reduced mangrove loss in Bangladesh, the United States of America, Pakistan and the Philippines (Fig. S6).

We found little evidence to suggest that the human footprint or cumulative marine pressures were related to mangrove loss at a global scale, however at a national scale, several nations showed strong relationships. A higher human footprint was associated with higher mangrove loss in Saudi Arabia, Thailand, the Philippines and Indonesia. Brazil exhibited an inverse relationship, where higher human footprint values were associated with lower loss (Fig. S7). Higher cumulative marine impacts in Bahamas, Vietnam, Indonesia, and Mexico had the strongest negative effects when compared with the global mean, suggesting that in these nations cumulative impacts on marine ecosystems are associated with more severe mangrove losses compared to other nations (Fig. S8). Counter-intuitively, Myanmar, the United States of America, Papua New Guinea and Brazil all had an inverse relationship that suggests reduced mangrove loss in landscapes with higher cumulative marine impacts (Fig. S8), however this may reflect areas where poor water quality (e.g. high sedimentation) may actually enhance mangrove establishment.

3.3. Systematic variation of landscape-scale effects of pressures and protected areas with national scale drivers

Overall, we found strong evidence for cross-scale interactions between national regulatory quality, and both population density and protected area coverage (Table 3; Fig. 5A, B), suggesting that the regulatory quality of a nation influences how these landscape-scale covariates affect mangrove forest loss. Higher population densities were associated with greater mangrove loss in nations with low regulatory quality when compared to nations with high regulatory quality (0.95 probability - Fig. 5A, Table 3). The reverse relationship was found for the interaction between regulatory quality and the effect of PAs, whereby greater protected area coverage had a stronger effect at reducing mangrove loss in nations with lower regulatory quality than in nations with high regulatory quality (0.89 probability - Fig. 5B, Table 3). There was no evidence (0.56 – indicates probability is only slightly better than random) to suggest that estimated national mangrove loss was directly related to national regulatory quality (Fig. 4).

4. Discussion

Globally, humans are placing unprecedented pressure on marine and terrestrial ecosystems (Jones et al., 2018; Halpern et al., 2019). Here we identified several associations between drivers, pressures, management responses and mangrove losses using globally available data. At a global scale, more fragmented mangrove forests in 1996 were

<table>
<thead>
<tr>
<th>Covariate</th>
<th>2.5%</th>
<th>( \Omega_{\text{eq}} ) (50%)</th>
<th>97.5%</th>
<th>( P(\Omega_{\text{eq}} \neq 0) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fragmentation</td>
<td>0.06</td>
<td>0.09</td>
<td>0.11</td>
<td>( P &gt; 0 = 0.99 )</td>
</tr>
<tr>
<td>Population density</td>
<td>-0.05</td>
<td>-0.02</td>
<td>0.02</td>
<td>( P &lt; 0 = 0.84 )</td>
</tr>
<tr>
<td>Protected areas</td>
<td>-0.02</td>
<td>0.01</td>
<td>0.04</td>
<td>( P &gt; 0 = 0.78 )</td>
</tr>
<tr>
<td>Terrestrial human footprint</td>
<td>-0.03</td>
<td>0.00</td>
<td>0.02</td>
<td>( P &gt; 0 = 0.61 )</td>
</tr>
<tr>
<td>Cumulative marine impacts</td>
<td>-0.04</td>
<td>-0.01</td>
<td>0.02</td>
<td>( P &lt; 0 = 0.69 )</td>
</tr>
</tbody>
</table>
positive outcomes for nations undergoing mangrove habitat change. Under canopy (Brinck et al., 2017). Our findings suggest that larger carbon stocks can be up to 50% lower at forest edges compared to accessible to anthropogenic disturbances, and are at greater risk to extreme weather events that may cause further mangrove forest loss (Li et al., 2020). Increasingly fragmented mangrove forests are more accessible to anthropogenic disturbances, and are at greater risk to extreme weather events that may cause further mangrove forest loss (Brinck et al., 2017). Our findings suggest that larger mangrove patches may be more resilient to pressures, and contribute to positive outcomes for nations undergoing mangrove habitat change.

Our findings of higher rates of mangrove loss near higher human population densities are consistent with the earlier literature (Richards and Friess, 2016; Allan et al., 2017). In one of the world’s largest mangrove forests, the Sundarbans, for every 1% increase in nearby human population density, an estimated 0.55% of mangrove area is lost through conversion to aquaculture (Kumar, 2012). Similarly, higher rates of population growth are associated with higher rates of deforestation in the Colombian Amazon (Armenteras et al., 2006). Human population density is associated with mangrove loss because agricultural expansion, infrastructure development and extractive use are generally associated with the needs of growing, dense populations (Geist and Lambin, 2001; Richards and Friess, 2016).

Increased protected area coverage was weakly associated with lower mangrove loss, a finding that is consistent with deforestation patterns of both mangroves and tropical forests more generally (Spracklen et al., 2015). For example, in Colombia, Panama and Costa Rica, 75% of mangrove deforestation has occurred outside PAs (López-Angarita et al., 2018), whereas in Indonesia and Brazil not all types of PAs adequately protect mangrove forests (Miteva et al., 2015; de Almeida et al., 2016). National variation in the effectiveness of PAs suggests that PAs alone should not be used to measure conservation success. Further, PAs are not effective for mitigating threats like climate change (e.g. sea level rise, extreme climate events), or pollutant runoff (Allison et al., 1998).

The lack of global scale relationships between mangrove loss rates and both the human footprint (Venter et al., 2016) and cumulative marine impact layers (Halpern et al., 2008) is not surprising. Coastal habitats lie at intersection of marine and terrestrial ecosystems so neither marine nor terrestrial cumulative impacts maps fully represent the issues they face, potentially explaining some of the spurious national-scale relationships. For instance, the marine cumulative impacts map uses human population density as a proxy for a range of threats to mangroves, including deforestation and seawalls. There is an urgent need to improve the scale of pressure mapping for coastal habitats, specifically for barriers to migration direct threats like conversion to aquaculture. Coastal specific threat maps will hopefully improve the accuracy of predictions of loss rates and thus have greater utility for informing coastal management.

### 4.1. Responses to landscape-scale pressures and management responses

We found that mangrove fragmentation was the most influential variable for all nations analysed in the current study. Habitat fragmentation is a major threat to the long term stability and function of mangrove forests (Haddad et al., 2015; Hauser et al., 2017; Bryan-Brown et al., 2020). Increasingly fragmented mangrove forests are more accessible to anthropogenic disturbances, and are at greater risk to extreme weather events that may cause further mangrove forest loss (Li et al., 2013). The consequences of forest fragmentation can be ecosystem wide, as carbon stocks can be up to 50% lower at forest edges compared to under canopy (Brinck et al., 2017). Our findings suggest that larger mangrove patches may be more resilient to pressures, and contribute to positive outcomes for nations undergoing mangrove habitat change.

Our findings of higher rates of mangrove loss near higher human

### Table 3

Parameter estimates for the slopes of the upper level regression quantifying cross-scale interactions between regulatory quality and each covariate in the DPSIR model ($\Omega_k$) with 95% Credible Intervals, and the one-sided probabilities of $\Omega_k$ being either less than, or greater than zero ($P(\Omega_k \neq 0)$). These coefficients quantify how the relationship between mangrove loss and each covariate changes as regulatory quality increases.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>2.5%</th>
<th>$\Omega_k$ (50%)</th>
<th>97.5%</th>
<th>($P(\Omega_k \neq 0)$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fragmentation</td>
<td>−0.04</td>
<td>−0.02</td>
<td>0.01</td>
<td>P &lt; 0 = 0.88</td>
</tr>
<tr>
<td>Population density</td>
<td>−0.01</td>
<td>0.03</td>
<td>0.07</td>
<td>P &gt; 0 = 0.95</td>
</tr>
<tr>
<td>Protected areas</td>
<td>−0.06</td>
<td>−0.02</td>
<td>0.01</td>
<td>P &lt; 0 = 0.89</td>
</tr>
<tr>
<td>Terrestrial human footprint</td>
<td>−0.04</td>
<td>0.00</td>
<td>0.03</td>
<td>P &lt; 0 = 0.61</td>
</tr>
<tr>
<td>Cumulative marine impacts</td>
<td>−0.06</td>
<td>−0.02</td>
<td>0.02</td>
<td>P &lt; 0 = 0.85</td>
</tr>
</tbody>
</table>

consistently related with greater overall mangrove loss in 2016. National variability in the effect of pressures and management responses on mangrove loss was also observed. National regulatory quality was not related to national-scale estimated losses; however there was evidence for interactions between national regulatory quality and the effects of both population density and protected area coverage. These findings highlight that the same pressures and responses may have very different impacts in nations under different regulatory conditions. This reinforces the importance of not relying solely on global-scale data to inform on national progress towards mangrove conservation.

### 4.2. Systematic variation of landscape-scale effects of pressures and protected areas with national scale drivers

We found strong evidence that both population density and...
protected areas interacted in a multi-scaled manner with national regulatory quality. First, higher population densities were associated with greater losses in mangrove forests in low regulatory quality nations compared to those with higher regulatory quality. A similar pattern was observed by Jha and Bawa (2006) in terrestrial biodiversity hotspots, where high human population growth in less developed regions was associated with higher forest loss. These patterns in forest loss may be caused by a greater dependency on mangrove forests for resources in nations with lower regulatory quality when compared to nations with higher regulatory quality (Barbier, 2010). For example, in Cameroon, the primary driver of mangrove deforestation is timber harvesting for fish smoking (Feka and Manzano, 2008). Similarly, in Kenya, rapidly growing populations exert heavy pressure on mangrove forests due to a strong reliance on mangrove wood products for fuel and building (Abuodha and Kairo, 2001). Finally, poorer countries (per capita GDP was highly correlated with regulatory quality) may convert mangroves into farming land (i.e. aquaculture or agriculture) out of necessity to generate income (Ewers, 2006).

We found that mangrove loss rates were lower inside PAs when compared to forests outside PAs, but only in nations with low regulatory quality. This finding is counterintuitive because nations with low regulatory quality may be expected to have the weakest enforcement of PA laws. However, in many countries mangroves are protected outside of PAs by strong legislation, such as that for protecting fish habitat (Barbier, 2010). Therefore, our findings suggest that PAs play a more important role in mangrove conservation in nations with low regulatory quality, whereas nations with high regulatory quality can enforce legislation that protects all mangrove forests. Our findings about PA effectiveness are consistent with local scale studies. For instance, land-use change is a primary cause of mangrove loss outside of protected areas in Honduras (Tubolske et al., 2017), and in south-east Asia (Richards and Friess, 2016). In Australia, which has high regulatory quality, the leading cause of mangrove loss is climate events that impact mangroves regardless of their protection status (Duke et al., 2017). An international scale review of policy and legislation is now needed to improve the accuracy of global scale mangrove forest predictions, because clearly PAs are only one of many important management tools for mangroves.

4.3. Limitations, research gaps and future directions

Many of the correlative relationships we observed were weak, and exhibited considerable uncertainty. This was not surprising, considering we were attempting to represent complex political and socio-ecological relationships at multiple scales using broad, globally available data. Regardless, this approach is useful because we highlight multi-scale interactions that suggest the same pressures and responses may have very different impacts when considered against national contexts. A key gap in existing pressure maps for mangroves is the lack of globally available predictors for the likelihood of land conversion to activities such as rice farming, aquaculture, or oil palm plantations. These activities often occur on rural coastlines, so are not expected to be related strongly to human population density or any of the other pressure indicators we used. The lack of a covariate representing the chance of conversion to these types of activities likely explains some key differences between the modelled mean landscape loss rates and the rates of loss observed in the data, especially for Bangladesh, Myanmar and India, where aquaculture is a significant contributor to mangrove deforestation (Kumar, 2012; Ahmed and Glaser, 2016). The conversion of mangroves for agriculture on rural coastlines may also explain why low cumulative impacts were associated with higher rates of loss in some countries (namely Indonesia). This gap in pressure maps for mangroves may be addressed by using the latest data on recent changes in aquaculture trends (Richards and Friess, 2016) to develop models that can predict the likelihood of aquaculture conversion on the basis of geopolitical covariates and account for the non-linear, slowing rate of
aquaculture expansion.

We applied the DPSIR framework here, and future work should expand our models to consider the ecological, social and economic impacts of mangrove loss. We demonstrate the utility of applying statistical modelling within a qualitative threat-impact-response framework to quantify indicators of change at two spatial scales (sensu Rhodes et al., 2017). Including impacts into future models will help inform how conservation management and pressures relate to outcomes for ecosystems and people, which are of most direct management relevance (Brander et al., 2012). Advancing our framework to consider socio-ecological change will require additional indicators, such as the recently developed mangrove socio-economic index, which considered the benefits of mangrove forests such as fishing and education, though currently only at local scales (Faridah-Hanum et al., 2019). Our model could also be expanded to consider the benefit of protecting mangrove forests for carbon storage (Atwood et al., 2017).

Further in-situ studies are needed to determine the causes of the associations we observed. For instance, increased habitat fragmentation was associated with greater rates of loss, but is not clear whether loss is caused directly by fragmentation, or whether fragmentation is simply an indicator of other processes that relate to greater mangrove loss, like harvesting of wood (Li et al., 2013). Further studies are needed to...
understand how ecosystem threats cause, or are exacerbated, by fragmenta-
tion. Future analysis should also explore how variation in capacity to manage PAs may alter the effectiveness of these areas for mangroves (e.g. McNally et al., 2011; Gill et al., 2017), in addition to quantifying the global effectiveness of management outside of PAs. Finally, there remains a need to assess how governance and management characteristics address threats from external sources that affect mangroves. A future research priority is therefore to better understand how global and national policy protect mangroves from these threats.

5. Conclusion

Using a Bayesian multi-scale approach, we were able to estimate how indirect pressures and management responses influence mangrove loss, while providing estimates of uncertainty in relationships at both national and global scales. Some large differences in the direction and magnitude of relationships between nations highlight that large-scale aggregated metrics of pressures on ecosystems may be inadequate for guiding management at national scales (Maréchaux et al., 2017). Global progress towards mangrove conservation will benefit from developing solutions that consider national context and address differences in the effect of pressures and protected areas on mangrove forests.

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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