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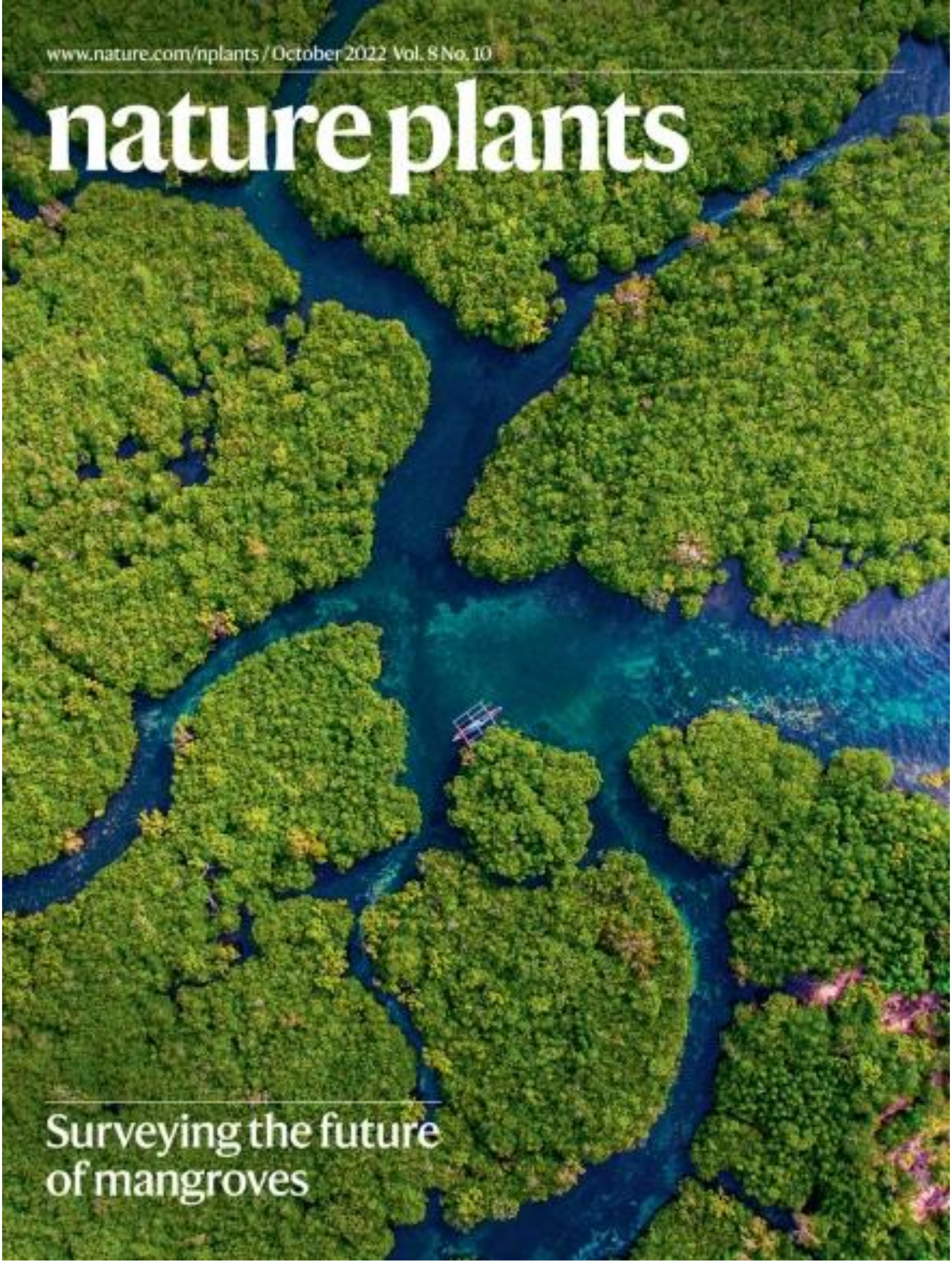

Surveying the future of mangroves

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Cross-cutting research themes for future mangrove forest research

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We identified the function of mangrove ecosystems that underpin ecosystem services, their responses to extreme weather and climatic events, and their role as crucial social-ecological systems as important paradigms shaping mangrove research now and in times to come. Since themes around functions and connectivity, ecological resilience to extreme events, and human–environment interactions are likely to be important underpinnings for other coastal and terrestrial ecosystems too, this paper aims to promote discussion within and beyond the mangrove research community and to help the broader plant science field in viewing and understanding the issue of safeguarding mangrove forests for the future.

Mangrove ecosystems are an important component of many tropical, subtropical and warm temperate coastlines. They provide habitats for terrestrial and marine biodiversity[1], and a range of ecosystem services such as shoreline protection[2], fisheries[3] and cultural services (for example, (eco)tourism)[4]. As such, mangroves are a key foundation of social-ecological resilience for coastal and global communities[5].

The perception of the social and ecological importance of mangrove ecosystems has changed over time, and as a result mangrove science has experienced several shifts in framing. Historically, they were often considered a source of disease and danger, or as an area of low value to be exploited[6]. Observations, experiments and analyses of mangroves intensified from the early 20th century when the initial focus was on ecological and biogeomorphological processes[7]. Several paradigms in mangrove science have since risen in importance, and old assumptions continue to be challenged and re-evaluated[8]. Studies from the 1960s emphasized ecosystem productivity and energy fluxes, and suggested that mangrove forests were carbon sources and sinks with high-carbon storage and potential high rates of carbon sequestration. Academic and applied interest in mangrove ecosystems has increased, particularly over the last decade, with mangrove 'blue carbon' now a focal paradigm. This refocusing of mangrove carbon dynamics addresses the urgent need to mitigate climate change and contributes knowledge that facilitates climate change adaptation and the supply of other ecosystem services.

While different aspects of mangrove research have risen in prominence, there are key foundational topics that (should) apply to all of them. Here, we propose three broad cross-cutting themes important in shaping mangrove research paradigms now and into the future: mangrove ecosystem functions underpinning ecosystem services, their responses to extreme weather and climatic events, and their role as crucial social-ecological systems. We identified these themes using our long-standing expertise in diverse academic disciplines and by following several focus group discussions. Ecosystem functions underpin the very ecosystem services that mangroves provide to local and global communities, yet remain poorly documented at local scales[2]. Extreme events and natural processes exacerbated by climate change already impact mangroves, and their influence is increasing relative to anthropogenic processes[9]. Socio-ecological perspectives are important, because a large proportion of the world's mangroves are used and impacted by people. Socio-ecological processes are relevant for the management and conservation of mangroves, and link mangrove science and application. Themes around functions and connectivity, ecological resilience to extreme events and human–environment interactions are likely to be important underpinnings for other coastal and terrestrial ecosystems too, so we intend to promote discussion within and beyond the mangrove research community.

Functional mangroves: seeing past the trees and beyond the forest

The functional ecology of mangroves defines the important processes underpinning ecosystem service provision. There is a substantial body of botanical and ecological knowledge about mangrove plants, with good knowledge of growth rates, reproductive strategies, adaptation to their brackish environment and biogeography. Plant responses to, and recovery from pollution are also well studied. The taxonomy and autecology of diverse invertebrate communities of mangroves has long received attention[10]. Research on food webs and carbon flows initially focused on outwelling of mangrove carbon as support for adjacent estuarine fisheries and later focused on inwelling of carbon in certain regions[11]. Over the last decade, the focus shifted concertedly onto the organic carbon retained in the forest, and we now have a solid understanding of the sequestration and cycling of carbon, and its global distribution[12].

An important recent lesson from marine ecological theory is that the positioning of habitats within the wider landscape and seascape profoundly influences ecosystem function[13]. This emerging concept is being deliberated in mangrove science, particularly the importance of the size, shape and positioning of mangrove patches, and their connectivity with other coastal ecosystems. For example, in estimating the value of mangroves in supporting fisheries' productivity, there is evidence that most fisheries species utilize a variety of ecosystems at different life stages, each critical to harvestable fisheries biomass[14]. Dissolved carbon fluxes are also influenced by connectivity between habitats[15]. The juxtaposition of habitat patches such as mangroves, seagrass beds and coral reefs is thus fundamentally important to the provision of ecosystem services and resilience. Connectivity and isolation among patches of mangroves themselves are also likely to be important; many mangrove forests are naturally fragmented, and human-driven habitat fragmentation has intensified[16]. Yet remarkably little is known about how mangrove fragmentation and altered connectivity affect service provision of either natural or rehabilitated mangroves. Increasing mangrove fragmentation also increases, for example, distances among natural populations of mangrove-associated invertebrate fauna and disrupts genetic flow among populations, ultimately impairing their viability[17]. Larval connectivity among mangrove patches is critical for the diverse populations of crustaceans and molluscs. These specialized invertebrates cannot necessarily be rehabilitated or restored through plantation efforts[18], but are critical to ensure mangrove functionality.

A recent theoretical approach to evaluating habitat vulnerability to global change is to assess organism traits rather than phylogenetic or taxonomic identity. Morphological and functional traits of species reveal their ecological functions and their role in the ecosystem. This approach has proved effective in predicting community structure[19] and species responses to gradual warming or heatwaves[20]. Preliminary research on morphological or functional traits of flora and fauna in mangrove forests is promising. Mangrove forests composed of trees with contrasting functional traits store more carbon than mangrove patches with low functional diversity, suggesting that best practices in mangrove restoration should focus on tree species functional diversity[21]. Mangrove fauna are characterized by unusually low functional diversity and redundancy[10], so modest local losses of invertebrate diversity could have significant negative consequences for mangrove ecosystems. Further research based on organism traits is necessary to estimate the health of natural forests and should be integrated in schemes aiming to assess mangrove degradation, as well as to design and evaluate rehabilitation or restoration projects[22].

Extreme events and interacting stressors

Mangroves exposed to extreme weather impacts, such as high winds and extreme precipitation, river flows, wave energy and storm surges, may recover from gross physical damage either by re-sprouting and rapid growth of existing seedlings, or by post-storm supply of propagules[23]. When physical damage is substantial, supply of organic material to substrates from living mangroves is reduced, and ensuing peat or organic matter collapse leads to rapid lowering of substrate elevations, decreasing the resilience of mangrove forests to subsequent extreme weather and to sea-level rise. Storm-induced geomorphological and hydrological changes are typically the cause of slow or absent recovery; sediment pulses that bury aerial roots and impounded tidal waters[23] can reduce oxygen availability within substrates. This leads to mangrove dieback, lowering of substrate elevations and increased vulnerability to subsequent events. Occasionally, extreme events improve mangrove resilience when pulses of sediment supply nutrients that enhance productivity or increase substrate elevations[23]. Recovery is dependent on i) species composition and structural complexity of mangrove forests, as species vary in their resilience to forces associated with extreme events[24] and ii) time between extreme events, as rapid recovery by some species has a lasting influence on canopy structure when events increase in frequency. Accordingly, mangrove forest structure pre- and post-extreme events influences recovery trajectories, has lasting implications on adaptation to frequent or compounding extreme events and alters the long-term capacity to provide ecosystem services. Collectively, these recent advances in our understanding of forest resilience help to inform conservation strategies and can also aid planning of emerging eco-engineering strategies for coastal restoration.

Unlike extreme weather events, climatic extremes are often cyclic and related to ocean–atmosphere interactions that cause climatic variability. Associated extended periods of drought, flooding and extremes in temperature alter the health and function of mangroves[25]. For example, climatic extremes resulting from negative phases of El Niño Southern Oscillation (ENSO) has caused flooding-induced dieback of mangroves throughout Africa, arising from extended periods of strongly reducing soil conditions[26], and caused drought-induced dieback throughout Australia, arising from lower rainfall and sea levels[27]. The coincidence of negative phases of ENSO and Indian Ocean Dipole caused severe rainfall deficits, elevated temperatures and lowered sea levels across Northern Australia, causing extensive mangrove dieback of >80 km^2. Similarly, the coincidence of ENSO and North Atlantic Oscillation has been implicated in severe freeze events across North America, which result in periodic physical damage, and a severe decrease in mangrove extent[28]. The devastating effect of recent coincident events has surprised researchers, as abrupt changes were not anticipated to occur so early along a trajectory of human-induced climate change. Advances in remote sensing technology and data accessibility have been accelerating, but still lack early warning systems that alert declining ecosystem health and function in advance of devastating effects[29].

The increasing occurrence and severity of extreme events in Earth's climatic future will confound projections of mangrove ecosystem health and function globally, and will poses considerable risk to the ecosystem service supply (Fig. 1). This is particularly concerning as many services provide negative feedbacks that influence climate mitigation and adaptation. While some extreme climatic events modulate the effects of climate change, these benefits may be short in duration (for example, the periodic regional decreases in sea levels associated with droughts that dampen the longer-term impacts associated with sea-level rise[24]) or limited in geographic range (for example, the reduction in frequency of freeze events and the increase in hurricanes implicated in the range expansion of mangroves at high latitudes in the northern hemisphere[28]).

The greatest risk for mangroves arises when extreme events periodically intensify climate-change impacts or when concomitant events occur. Critically, these risks will impact mangrove forests where resilience is already limited by human impacts and pressures; reducing these will increase the resilience of mangroves to extreme events[30]. Projections of mangrove forest responses to sea-level rise have been undertaken for several decades; however, modelling tolerance thresholds to temperature and sea-level rise are still in early stages[31], and rarely include extreme events as stressors. Emerging evidence of transitions from ecosystems maintained by negative feedbacks to destabilization of processes and dominance of positive feedbacks[32] emphasizes the urgent need to investigate the role of extreme events in modulating tolerance thresholds. We anticipate the ability of climate modellers to project extreme events will continue to improve, and research of mangrove resilience should focus on coupling models of mangrove response to multiple stressors. In the meantime, monitoring the impact of extreme events on mangroves will be crucial for parameterising coupled models once they are available. Research networks and collaborations that are inclusive, diverse, geographically representative

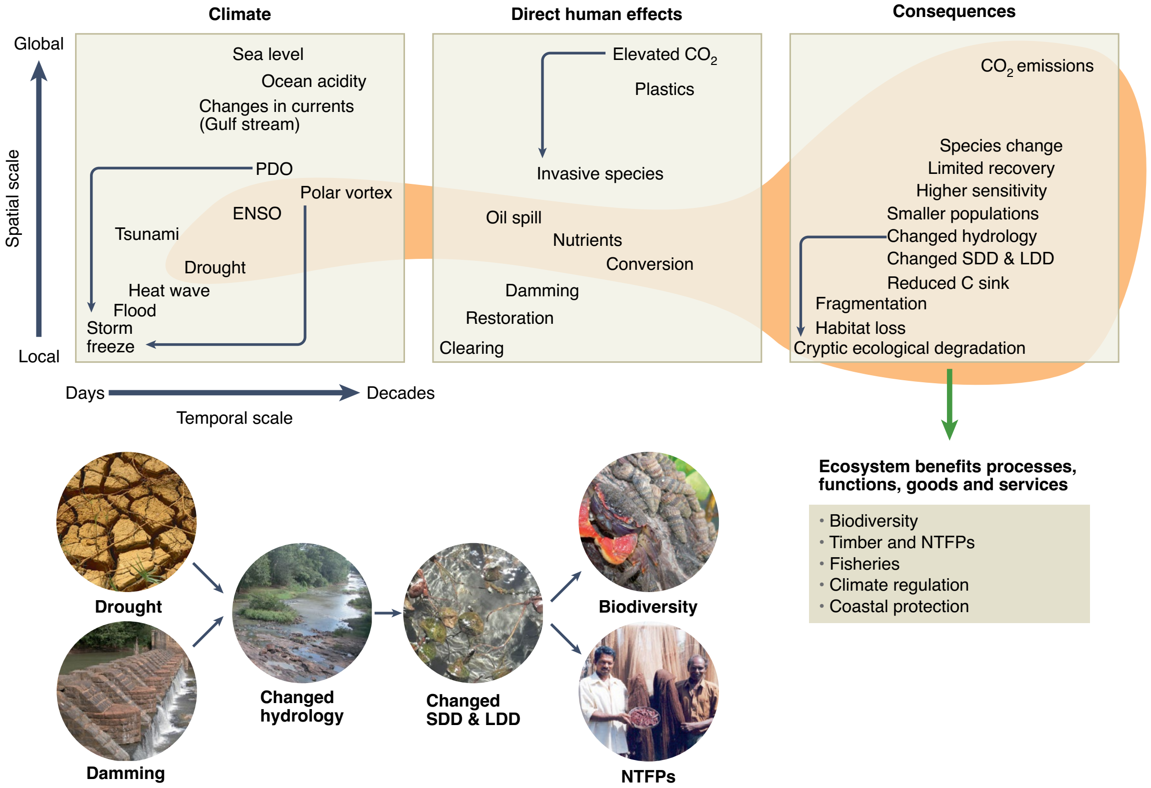

Fig. 1 | Spatio-temporal diagrams of climate, direct human influences and their consequences, exemplifying how they in turn (green arrow) affect mangrove ecosystem benefits. The black arrows in the boxes exemplify the influence of larger global scale cycles or impacts on shorter cycles and more local processes; for example, climatic oscillations such as the ENSO changes in frequency of storms and precipitation patterns, polar vortex affects freezes, elevated CO_2 facilitates species invasions and changed hydrology that may trigger cryptic ecological degradation[29]. The orange cloud demonstrates that factors at quite restricted spatial and temporal scales, such as a drought or conversion, can have long-term and global effects on ecosystems; for example, conversion of mangroves leads to CO_2 emissions that stay in the atmosphere forever and to fewer fish in a wide range of habitats beyond the mangrove. The inset box with photographs provides a more linear example of how the combination of drought and damming of rivers affects river hydrology, which in turn changes short distance dispersal (SDD) and long distance dispersal (LDD) of species (*Xylocarpus granatum*), resulting in changed species diversity and/or behaviour (*Neosarmatium africanum* and *Cerithidea decollata* stuck on mangrove roots and stems during high water contribute to leaf fragmentation and propagule predation at low water) and to provision of non-timber forest products (NTFPs) used in artisanal fisheries. PDO, pacific decadal oscillation. Photo credits and/or copyright from left to right and from top to bottom: Michele D'Amico supersky77 / Moment / Getty, Farid Dahdouh-Guebas (Sri Lanka, 2004); Farid Dahdouh-Guebas (Sri Lanka, 2004), Farid Dahdouh-Guebas (Malaysia, 2016), Stefano Cannnicci (Kenya, 2004), Dahdouh-Guebas et al.[40] (India, 2001).

and interdisciplinary will strengthen capacity to project the response of mangroves to compounding extreme events and will implement appropriate planning and management actions that improve resilience and restore ecosystem function.

Mangroves as social-ecological systems

Mangroves are social-ecological systems that provide provisioning ecosystem services, including food, fuel, construction materials and medicinal products. Mangroves also provide intangible and often under-recognized benefits related to cultural heritage and religious and spiritual values[5]. Conversely, people can also affect the ecological integrity of mangroves through overexploitation or through large-scale land use and land cover change[9]. Understanding mangroves as a social-ecological system allows communities, managers and policy makers to reconcile human use and the production of ecosystem services with the need to reduce their large-scale conversion and encourage sustainable and community-based natural resource management.

The monetary value of mangrove goods and benefits has been estimated regionally and globally[2]. However, broad averages per hectare hide substantial variation in ecosystem service provision between mangrove types and geomorphic settings[33], as well as the demand from resource users for the resulting goods and benefits, so have limited utility in socioecological assessments that are location- and context-specific. For example, the values of coastal protection and mangrove construction wood differs by an order of magnitude among countries[34]. The monetary value of mangrove tourism[4], as well as fishing intensity[3], can vary by two orders of magnitude. The physical, ecological, socioeconomic and governance factors driving variation in value remain largely unknown and should be a priority research topic.

It is important to include cultural services such as the spiritual significance of mangroves for coastal communities when valuing mangrove contributions to people, but methodologies to value intangible ecosystem services remain nascent. The worldview of coastal communities can help preserve mangroves by encouraging the incorporation

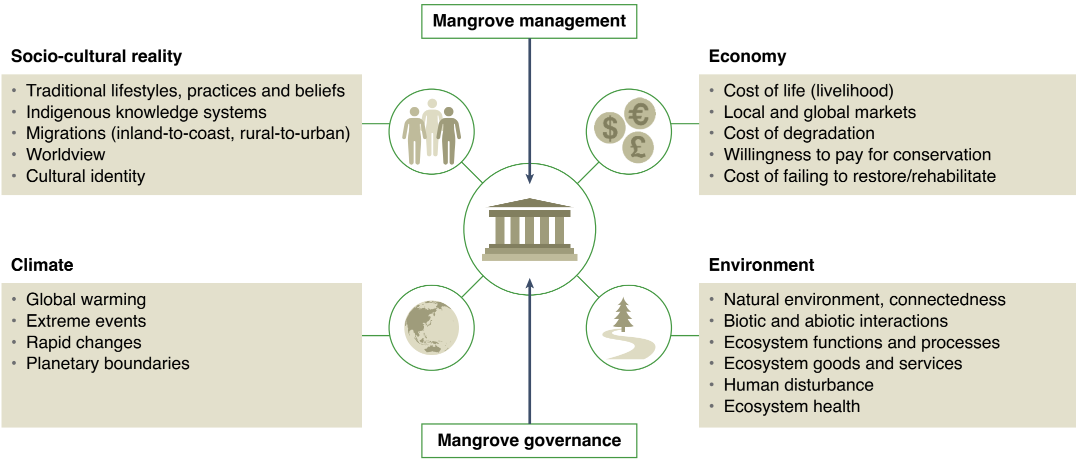

Fig. 2 | Reality framework showing that management and governance should be at the heart of a local community's socio-cultural, economic, environmental and climatic reality. Several constituents of these realities are still poorly known in mangroves.

of wider social values into management and decision making, or by integrating them as an additional cultural importance layer in valuation exercises, akin to that of the IUCN Red List of Threatened Species or Ecosystems. Mangrove management will benefit from consistent documentation and mapping of ecosystem service provision, using ethnobiological research to incorporate nuanced differences among communities in different places.

Deforestation and degradation patterns are driven predominantly by underlying socio-economic and governance drivers, and understanding these drivers enables consideration of future deforestation risk. Frameworks based on objectively verifiable indicators[22] could be extended to compare the cost of further degradation against that of restoration. Restoration policies and goals will need to incorporate social factors that limit the implementation of restoration and conservation initiatives. For example, ecosystem functions such as wave attenuation and carbon sequestration are increasingly used as justification for mangrove restoration, but obvious research gaps remain in the socio-economic sciences and humanities domains. Holistic studies mapping and integrating the benefits of coastal protection for human populations, which in turn depend on the number of lives, properties and investments that a mangrove forest buffers against ocean influences, are lacking. Similarly, the socio-economic implications of blue carbon initiatives for local communities remain poorly considered.

Incorporating knowledge of diverse social and cultural values, alongside monetary valuations, will also improve understanding of the demand for ecosystem services and inform the sustainable use of resources. Ethnobiological studies currently integrate non-timber forest products or cultural values[35]. A prerequisite to safeguard the supply of ecosystem services at local, regional and global levels is the integration of indigenous knowledge systems into management of mangrove forest resources, which could help bridge the divide that often exists between mangrove resource management authorities and mangrove-dependent communities[36]. To understand drivers of degradation and dependence of communities, we advocate further research into the ecological and social dynamics of mangrove utilization/dependency (for example, attrition of local and/or traditional ecological knowledge).

Ultimately, mangrove-resource use is shaped by local economic contexts within different management and governance regimes, which merit research attention. Local communities are often harmed by their government's own policies and practices, for instance, through political patronage[37], wrong practices[38] or poor land tenure regulations[39]. Scientific studies should first investigate country-specific managerial priority questions to which an answer is needed in the field (https://serm.ulb.be/mangrove-priority-questions/) and explore how results can be translated into meaningful (sustainable) restoration, management and governance policies and practices that account for the socio-cultural, economic, climatic and environmental reality of a local community (Fig. 2). These realities represent the endogenous and exogenous stressors and drivers of the social-ecological mangrove system.

Conclusion

Current and emerging paradigms in mangrove research, such as their role in carbon cycling and climate change mitigation, are now strongly influencing coastal management and policy. A focus on individual paradigms (often based around a single ecosystem service) risks ignoring key foundational information and data requirements that underpin multiple aspects of mangroves. The functionality of mangrove ecosystems, their response to extreme events and interacting stressors and their role as crucial social-ecological systems underpin or can contribute to previous, current and undoubtedly future research paradigms. However, our knowledge of these cross-cutting themes is not complete, and several research frontiers remain that will further improve our ability to understand and manage mangrove forests. Continued research into the themes identified here will help ensure that future research into mangroves is grounded and connected, and will ultimately refocus mangrove research and management around important themes of connectivity, ecological and human resilience.

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Author contributions

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Competing interests

The authors declare no competing interests.