CellPress
REVIEWS

Review

The Role of Vegetated Coastal Wetlands for Marine Megafauna Conservation

Michael Sievers,[1,*,@] Christopher J. Brown,[2] Vivitskaia J.D. Tulloch,[3] Ryan M. Pearson,[1] Jodie A. Haig,[1] Mischa P. Turschwell,[3] and Rod M. Connolly[4,5]

Habitat loss is accelerating a global extinction crisis. Conservation requires understanding links between species and habitats. Emerging research is revealing important associations between vegetated coastal wetlands and marine megafauna, such as cetaceans, sea turtles, and sharks. But these links have not been reviewed and the importance of these globally declining habitats is undervalued. Here, we identify associations for 102 marine megafauna species that utilize these habitats, increasing the number of species with associations based on current International Union for the Conservation of Nature (IUCN) species assessments by 59% to 174, accounting for over 13% of all marine megafauna. We conclude that coastal wetlands require greater protection to support marine megafauna, and present a simple, effective framework to improve the inclusion of habitat associations within species assessments.

Highlights

Marine megafauna and vegetated coastal wetland habitats (seagrasses, saltmarshes, and mangroves) are under intense threat and declining globally.

Emerging research and novel methodologies have unveiled important, previously unknown habitat associations between marine megafauna and these habitats.

Unless we can conceptualize and critically examine these habitat associations, management and conservation can be undermined.

Identifying threatened species that are dependent on threatened habitats is essential for informing on actions to prevent population declines.

Are Vegetated Coastal Wetlands Important for Marine Megafauna?

Marine megafauna (see Glossary) are globally recognized as providing significant economic, cultural, and ecological values [1,2]. Despite this, many have experienced population declines, putting some species at risk of extinction [3–5]. Emerging research and novel methodologies are finding important, previously unknown habitat associations between marine megafauna and **vegetated coastal wetlands** (seagrasses, mangroves, and saltmarshes; e.g., [6,7]), suggesting that these marine habitats are important in supporting and sustaining megafauna. However, vegetated coastal wetlands are also in global decline and there is an urgent need for effective management and conservation effort in these habitats [8–11]. The ability to implement management and conservation in marine systems is often impeded by incomplete understanding of species habitat requirements and critical ecological processes operating between species and habitats [12]. While coastal regions in general have been suggested as areas of conservation concern for marine megafauna [4,13], the importance of seagrasses, mangroves, and saltmarshes specifically is not currently well conceptualized for megafauna or their conservation.

Megafauna also fulfil important functions for coastal wetlands. Semiaquatic species link aquatic and terrestrial biomes by transporting nutrients across boundaries [14], while migratory species with large home ranges can disperse nutrients and plant propagules across wide areas [15–17]. Grazing of seagrass by turtles and dugongs can benefit seagrass communities by increasing nitrogen availability [18], and declines of these species have the potential to cause degradation of seagrass meadows [19]. Megafauna predators, such as sharks, also assist in maintaining and growing reserves of 'blue carbon' within coastal wetland habitats [20] and have important roles as apex predators in near-shore food webs [21].

To advance the global state of knowledge surrounding links between vegetated coastal wetland habitats and marine megafauna, we systematically classify habitat associations from the published literature (see Appendix A in the supplemental information online for methodology). Given

[1]Australian Rivers Institute – Coast and Estuaries, Griffith University, Gold Coast, QLD 4222, Australia
[2]Australian Rivers Institute – Coast and Estuaries, School of Environment and Science, Griffith University, Nathan, QLD 4111, Australia
[3]Australian Rivers Institute, Griffith University, Nathan, QLD, 4111, Australia
[4]Australian Rivers Institute – Coast and Estuaries, School of Environment and Science, Griffith University, Gold Coast, QLD 4222, Australia
[5]https://www.globalwetlandsproject.org/

*Correspondence:
m.sievers@griffith.edu.au (M. Sievers).
@Twitter: @SieversSci (M. Sievers).

the increasing global importance and use of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species database [22], we also critically evaluate species assessments for megafauna considered to have an association with these habitats and propose an updated framework for the inclusion of habitat data in assessments. It is timely that we review this literature to identify priorities for wetland research and evaluate how wetland protection can best serve megafauna.

Identifying and Defining Habitat Associations

Species conservation and protection, and the policy that enables these, relies on knowledge of how and which species utilize specific habitats. The standardization of habitat associations within IUCN species assessments also allows geographical and taxonomic comparisons to be made that are important for guiding conservation efforts and assessing conservation outcomes [23]. Inaccurate or missing information can compromise these efforts. For example, the often-cited statement that 'an estimated 75% of commercially caught fish depend directly on mangroves' [24] was recently determined to be wildly inaccurate and not based on definitive scientific evidence. The use of unsupported claims poses serious issues for conservation as hypotheses and arguments that are built upon it are weakened by the lack of scientific evidence and can be easily debunked [24].

Here, we classify habitat associations from the literature as: (i) occurrence: occurring within or directly adjacent to the habitat (e.g., GPS tracking of turtles within seagrass patches or observing dolphins along mangrove banks); (ii) grazing: directly consuming the habitat forming species (e.g., observing dugongs, *Dugong dugon*, consuming seagrass, or turtle stomach lavage samples containing mangrove fruits); (iii) foraging: hunting or scavenging within or directly adjacent to the habitat (e.g., rays foraging on invertebrates within seagrass meadows, or sharks hunting along the edges of seagrass meadows), or from the food web of the habitat (e.g., isotopic analyses identifying seagrass-associated prey forming part of the diet); and (iv) breeding: breeding occurring within the habitat or juveniles within sites that satisfy the requirements of a nursery habitat [25] (e.g., juvenile lemon sharks, *Negaprion brevirostris*, congregating within mangrove-fringed lagoons). We include 'directly adjacent to the habitat' because megafauna can, for example, hunt prey along mangrove-fringed shorelines without physically entering the small gaps within mangrove roots (although they can be above aerial roots without this being mentioned within studies).

Occurrence is considered an **indirect association** and the other classifications are **direct associations**. Direct habitat associations have varying strengths of evidence. That is, levels of **habitat dependency** are subject to gradation. For example, the level of dependency for sharks using mangrove-fringed lagoons as nursery areas is less clear than for dugongs consuming seagrass. It may be that the mangroves provide specific protection and prey resources, and are irreplaceable, but it may also be that sharks would just as readily and successfully use the lagoon as a nursery if a different vegetation type was present. Ideally, these classifications would feed into a quantitative assessment of how the habitat contributes to a species population growth rate and, thus, how habitat decline can increase the risk of extinction. Such quantitative assessments would require estimating differences in population demographic rates between locations or times with and without the habitat [26]. This can be relatively straightforward for species that are solely reliant on one food type (i.e., dugongs consuming seagrass), but very difficult for species that have a facultative dependence on the habitat.

Although our separation of habitat associations into direct and indirect provides an easy and informative means to assess habitat associations, we might also be overestimating the importance of coastal wetlands for some species, because evidence of associations from

Glossary

Direct association: where the animal directly utilizes the habitat as a food source, foraging ground, nursery, breeding area, or some other interaction beyond simply occurring within a habitat.
Habitat dependency: quantitative measure of how reliant an animal is on a specific habitat type (e.g., obligate habitat use).
Indirect association: a habitat association with no evidence of a direct association (e.g., occurrence).
Marine megafauna: primarily aquatic species from the following groups: sea turtles, whales, dolphins, porpoises, otters, minks, seals, crocodiles, alligators, dugongs, manatees, and sharks and rays (elasmobranchs).
Obligate habitat use: when a specific habitat type is fundamentally needed for the existence of an animal.
Remote sensing: the scanning of the earth by satellite or high-flying aircraft to obtain information about it, particularly in terms of habitat and vegetation mapping.
Stable isotopes: nonradioactive forms of atoms that can be used as indicators to trace the diet and habitat used by animals before the sampling period.
Telemetry: process of recording and transmitting the readings of an instrument, often used to track animal movements.
Vegetated coastal wetlands: three key vegetated coastal wetland habitats: seagrasses, saltmarshes, and mangroves: as defined by the Ramsar Convention (wetland categories B, H, and I, respectively): 'wetlands include a wide variety of inland habitats such as marshes, peatlands, floodplains, rivers and lakes, and coastal areas such as saltmarshes, mangroves, intertidal mudflats and seagrass beds, and also coral reefs and other marine areas no deeper than six meters at low tide, as well as human-made wetlands such as dams, reservoirs, rice paddies and wastewater treatment ponds and lagoons' [70].

these habitats might be an artefact of the surrounds or adjacent alternative habitats rather than of the habitat-forming species itself (e.g., mangroves [27]). Conversely, we might be dismissing key habitat associations as indirect due to a lack of supporting scientific data. For example, turtles can rest and find refuge among mangroves, and crocodiles use saltmarsh to bask, and these could be vital ecological functions provided by vegetated coastal wetlands, but are deemed as an 'occurrence' under our criteria. Hence, our occurrence data could be considered knowledge gaps, where data are still required to properly assess habitat association types.

Megafauna Associations with Vegetated Coastal Wetlands

Our review of 341 studies (Appendix B in the supplemental information online) identified 102 megafauna species associated with vegetated coastal wetlands (Appendix C in the supplemental information online). Associations were most commonly documented by visual observation (55%), electronic tracking (14%), or from dietary analysis based on gut contents (18%) or **stable isotopes** (11%). Less common methods (2%) included acoustic recordings, contaminant and fatty acid levels, and animal-borne video cameras. Many species had well-studied and important associations with coastal habitats (Figure 1). For example, seagrass is often the only dietary component for green turtles (*Chelonia mydas*) and dugongs [28,29], and this was well conceptualized and validated in the literature. Similarly, mangroves, saltmarshes, and seagrasses offer ideal hunting and foraging grounds for predators such as dolphins, sharks, rays, and crocodiles [30–32]. These habitats also function as nurseries where juveniles of species, such as critically endangered smalltooth sawfish (*Pristis pectinata* [33]), dugongs [34], and lemon sharks [35], seek refuge during vulnerable early life stages.

Sharks and rays were the dominant taxonomic group, contributing 66 of the 102 species from our literature review. This group was primarily associated with seagrass and mangroves, with most direct associations related to hunting within seagrass patches (18 species; Appendix D in the supplemental information online). Few megafauna were linked with saltmarsh (12 species), indicating that this habitat is relatively less important for megafauna or that it is less well studied. Overall, the most studied species in terms of number of studies identifying links were the bonnethead shark (*Sphyrna tiburo*), lemon shark, and smalltooth sawfish.

Of the 102 species identified from the peer-reviewed literature, 64 did not have any of the three habitat types recognized as a habitat within their IUCN assessment. Conversely, we identified 71 species with noted vegetated coastal wetland habitat associations from IUCN Red List assessments that were not identified in our search of the published literature. Evidence for IUCN associations were largely based on unpublished literature, personal observation, personal communication, and assumptions that the species would occur in the same habitat as congeneric species. In total, the 64 additional species we identified increase the number of marine megafauna with habitat associations with coastal wetlands by 59%, to 174 species (Figure 2). This considerable increase means that at least 13% of all extant marine megafauna species have some link with vegetated coastal wetlands (Figure 2).

The Importance of Habitat Associations in Assessments

IUCN Red Lists have become a go-to source of information used to guide species conservation [36,37]. The wealth of additional data collected during the assessment process, such as threats and habitat associations, is regarded as one of its most important features, insofar that these parameters are standardized to allow comparative analyses [38]. These can be used, for example, to compare trends for suites of species in different habitats. Red List threat categorizations also provide a baseline for measuring conservation responses [22]. For instance, conservation recommendations identified in assessments for globally threatened birds in 2000 resulted in two-thirds of threatened bird species having some of these actions implemented by 2004 [22,39].

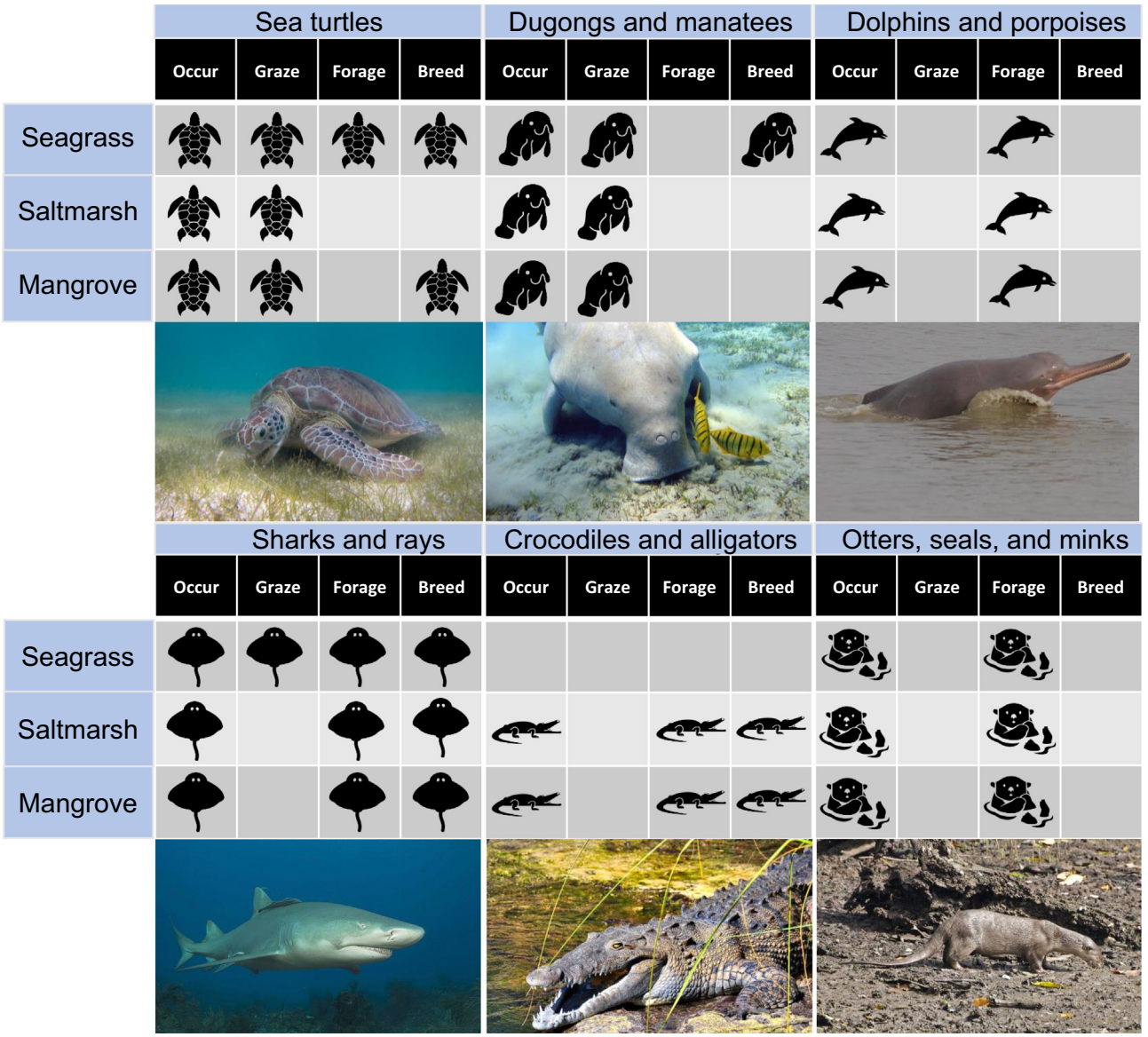

Figure 1. Marine Megafauna Habitat Associations with Vegetated Coastal Wetlands (Seagrasses, Mangroves, and Saltmarshes) Confirmed in the Peer-Reviewed Scientific Literature. Marine megafauna graze, forage, and breed in all three habitats, as indicated by symbols within the habitat-association matrix. We classify habitat associations from the literature as: (i) occur: within or directly adjacent to the habitat; (ii) graze: directly consuming the habitat forming species; (iii) forage: hunting or scavenging within or directly adjacent to the habitat, or from the food web of the habitat; and (iv) breed: juveniles within sites that satisfy the requirements of a nursery habitat or nesting within the habitat. All images are Creative Commons (CC) or Public Domain (PD). Sea turtles, P. Lindgren (CC BY-SA 3.0); dugongs and manatees, J. Willem (CC BY-SA 3.0); dolphins and porpoises, Z. Alom (PD); sharks and rays, A. Kok (CC BY-SA 3.0); crocodiles and alligators, Mattstone911 (CC BY-SA 3.0); otters, seals, and minks, L. K. Yap (CC BY-SA 2.0). Original images have been cropped.

Furthermore, habitat-based conservation actions are often recommended in Red List assessments for those species with strong habitat associations [22].

Despite important habitat associations identified in our literature review, IUCN assessments for 64 of the 102 species did not include any vegetated coastal wetland habitat (even though 32 species had direct associations). For example, green turtles often rest in mangroves and consume

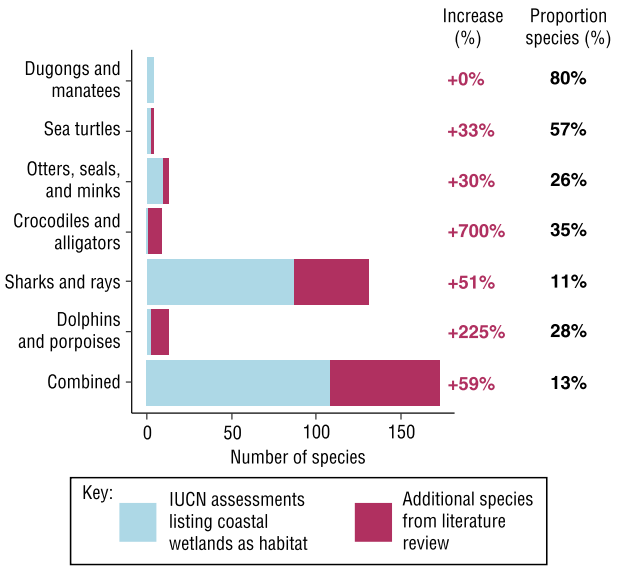

Figure 2. Summary Statistics from Reviewing the Literature and the International Union for the Conservation of Nature (IUCN) Database. The number of species identified as having a habitat association with seagrass, mangroves, or saltmarsh based on IUCN species assessments (blue bars) and those additional species from our literature review (purple bars). The resultant percentage increase in the number of species with habitat associations (Increase %) and the proportion of all species within key taxonomic groups that are associated with coastal wetlands (Proportion species %) are shown. Our literature review considerably increases the number of species with known habitat associations based on habitat data extracted from IUCN species assessments, potentially assisting conservation efforts given global declines in seagrasses, mangroves, and saltmarshes.

mangrove leaves and fruits [40–43], and bull sharks have strong links with mangrove estuaries as nurseries [26], yet mangroves are not currently identified as important for these species. In some cases, such as for many of the crocodiles and alligators, assessments are largely incomplete and were conducted before the studies that identified and published evidence of important habitat associations (Appendix C in the supplemental information online). Different forms of information are used to inform species conservation, such as expert knowledge and species distribution models. The information within IUCN assessments is also used to identify actions for threatened species management. Therefore, when species assessments overlook habitat associations, as we show currently occurs for 63% of the species identified, conservation may not be directed towards the most effective management actions, such as protecting habitats.

A Framework for the Inclusion of Habitat Data in Species Assessments

We argue that greater consideration of the role of vegetated coastal wetlands in the lives of many megafauna should be included in management and conservation plans for these species. Otherwise, valuable resources might be invested in ineffective conservation action that does not halt species decline. This is particularly important because almost half of these species are listed as threatened (Figure 3). Although IUCN assessments provide the opportunity to apply a ranking of habitat importance (e.g., 'suitability' and 'major importance?'), these are seldom included in assessments, are difficult to interpret, and do not offer the capacity to contrast direct or indirect habitat-associations.

The type of habitat association is important information that should be included in assessments as a priority whenever possible. At minimum, objective classification of the direct or indirect nature of each association for each habitat type should be articulated and supported by clear evidence.

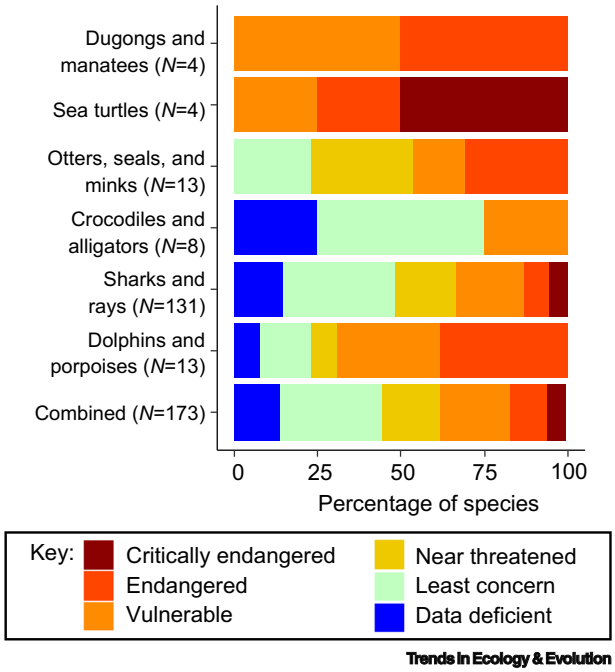

Figure 3. Vegetated Coastal Wetland-Associated Marine Megafauna International Union for the Conservation of Nature (IUCN) Threat Status. The percentage of species within key taxonomic groups as classified by the IUCN Red List of Threatened species categories. More than 50% of species are near threatened or worse, highlighting the critical need for conservation action for these animals and their habitats. Maskrays have been excluded from this figure because no status was assigned.

Ideally, we would also identify how reliant a species is on a habitat by estimating levels of dependency (e.g., **obligate habitat use**). Therefore, assessments would include: (i) all habitat types the species is known to associate with; (ii) the association type broadly categorized into occurrence, grazing, foraging, or breeding (or other relevant species-specific categories); (iii) where the evidence supporting this association comes from, and; (iv) an estimate of the level of habitat dependence. This provides transparent and useful information for achieving the many goals of the IUCN Red List, such as identifying knowledge gaps, guiding conservation research efforts, informing policy and conventions, and improving conservation planning and decision-making (see: www.iucnredlist.org/about/uses). Finally, many assessments should be updated as new information about habitat associations is published in the scientific literature. We acknowledge the considerable time and effort required to achieve these recommendations but argue that the benefit would significantly outweigh the time cost.

Bringing Habitat Loss and Degradation in Vegetated Coastal Wetlands to the Fore

Correctly identifying habitat associations will better inform impact assessments for habitat loss and degradation. These threats are prolific in coastal wetlands [44] and have significant effects on marine megafauna (Box 1). However, when threat data were presented for the 174 species associated with these habitats, 52% of the IUCN species assessments did not mention any form of human-induced habitat change. The effects of habitat change can be overlooked for marine animals [45] because of the sublethal, chronic effects that occur initially, and because impacts can be hard to directly attribute to species declines without long-term data sets separating natural fluctuations from the effects of human impacts [46].

Box 1. The Impact of Vegetated Coastal Wetland Loss and Degradation on Marine Megafauna

Reductions in the extent and condition of seagrasses, mangroves, and saltmarshes can impact marine megafauna by: (i) reducing the quantity and quality of food for herbivores; (ii) depleting prey availability for predators and scavengers; (iii) disrupting key life-history stages by limiting the availability or effectiveness of nursery and refuge areas; (iv) reducing the amount of suitable breeding habitat; (v) increasing interpatch distance and reducing habitat connectivity; and (vi) increasing species interactions with other anthropogenic stressors. Furthermore, the causal factors of habitat loss and degradation also affect megafauna directly (e.g., pollution, warming seas, fishing pressures, or exotic species introductions [58–60]). Habitat loss and degradation of coastal wetlands can impact marine megafauna through complex multistressor interactions. For example, increased fragmentation or decreased quality of seagrass beds forces herbivores to travel farther to find high-quality food patches to fulfil their daily energy requirements [61]. Doing so can increase the risk of boat strikes, a leading cause of mortality [62,63]. We could infer that by reducing the causes of seagrass fragmentation and degradation (e.g., improving water quality or minimizing coastal development), seagrass beds would become denser and more connected, which would serendipitously reduce the risk of boat strikes. Thus, the benefit of actions on habitat quality has an additional, but largely unidentified, benefit in terms of reducing boat mortalities. Saving habitat and protecting remaining habitat from other stressors (e.g., boat no-go zones) could be the 'silver bullet' for conservation of marine megafauna.

Furthermore, threatening processes are also context dependent, where localized threats, such as the construction of a port or nutrient discharge from a heavily urbanized estuary, can disproportionately affect species with lower capacity to move away from the threat. By contrast, far-ranging species, such as dugongs, which are not necessarily dependent on specific habitat patches for food, will generally be less affected by localized disturbances [64]. This contrasts with many far-ranging, migratory terrestrial species that do rely on specific coastal wetlands as breeding grounds, where localized habitat loss and degradation can cause significant population declines (e.g., migratory birds breeding in saltmarsh habitats [65]). This highlights several important considerations when designing conservation and management initiatives for marine megafauna. Irrespective of life-history strategies, when threats occur over large geographical areas, such as those due to human-induced climate change, the impacts of habitat loss and degradation are likely to affect a large number of species [66].

This is particularly true for sharks and rays, the largest group of species without habitat change listed as a threat. For this group, fisheries pressures, which are comparatively more straightforward to quantify and interpret, were often listed as a threat. However, it is important that we assess and quantify relationships between megafaunal demography and changes in coastal wetlands for those species with known habitat associations. This is especially true for the persistence of harvested megafauna (i.e., fisheries species) with critical life-history links to threatened habitats, because, under this scenario, fishery management alone may be insufficient to prevent population declines [45]. In this case, incorporating habitat change into conservation assessments and management plans could be achieved by recognizing the importance of vegetated coastal wetlands to marine megafauna and conducting robust research into the habitat associations that exist. This will assist in the protection of not only the economically and ecologically important megafauna, but also the numerous co-benefits to humans (including many ecosystem services) provided by vegetated coastal wetland [47,48].

Existing and Emerging Techniques

Much can be done to address gaps between species conservation and habitat change, and future research would do well to further utilize both existing and emerging technologies. Recent advances in **remote sensing** have enabled the development of spatially explicit, high-resolution global data sets on the distribution of, and rates of change in, ecosystems and habitats (Box 2) [49]. Coupled with modern computing capacity and analytical tools, models and predictions of how habitat change alters species occurrence, distributions, and extinction probability [38,50] can be made if robust information about habitat associations along with the strength and importance of these associations is known. This information directly feeds into species assessments and spatially explicit species conservation, improving outcomes [51,52]. Although this level of knowledge remains elusive for many taxa, advances in commonly used techniques, such as **telemetry**, capture–mark–recapture, video (stationary and animal-borne), and stable

Box 2. Global Biodiversity of Vegetated Coastal Wetland-Associated Marine Megafauna and Hotspots of Conservation Concern

Coastal wetland-associated megafauna biodiversity was highest in Southeast Asia, northern Australia, the east and west coasts of Africa, the southern USA, Central America, and northern South America (Figure I). Conservation outcomes can be improved and made more efficient by identifying hotspots where high concentrations of threatened native species intersect with habitats that are being lost and degraded [67]. High rates of mangrove loss intersected with threatened megafauna distributions most strongly in Southeast Asia, Florida (USA), Mexico, and northern Brazil (Figure I). Southeast Asia is the largest mangrove-holding region of the world, and mangroves are being lost at rates far exceeding global averages [68], largely due to aquaculture and agriculture [69]. Brazil and Mexico are also mangrove-rich countries [68], and guiding protection and restoration of mangroves towards these hotspots will assist in the conservation of threatened marine megafauna that utilize these important habitats.

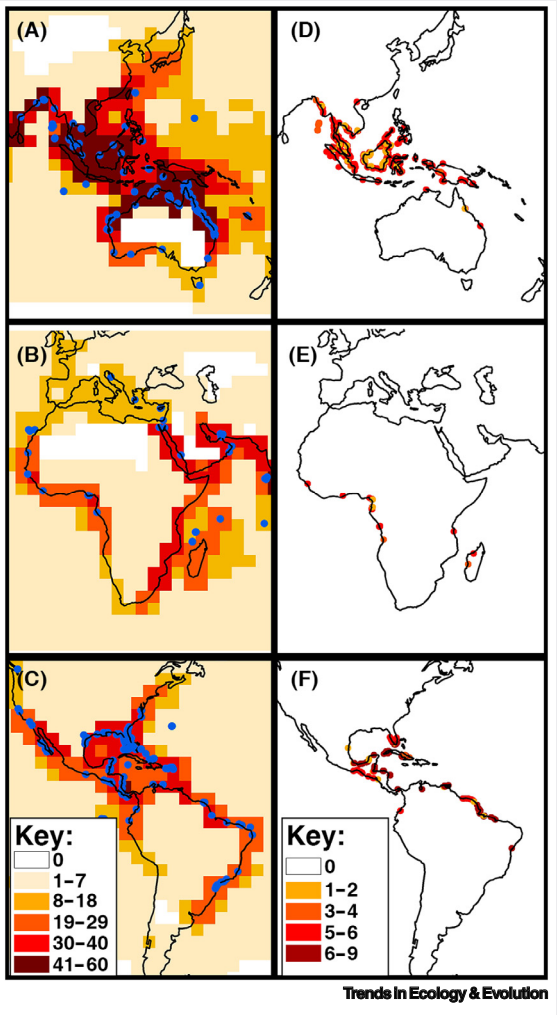

Figure I. Vegetated Coastal Wetland-Associated Marine Megafauna Distributions across Three Key Geographical Regions. Heatmaps of biodiversity for 172 of the 174 marine megafauna identified as having an association with seagrasses, mangroves, or saltmarshes for the three geographical regions with the most species [to aid visualization; (A) Asia Pacific; (B) Africa and Europe; and (C) North and South America]. The blue dots represent locations of field studies from the literature review, and the graded colors represent species richness (see Key). Note that the distributions of some species (e.g., otters and caiman) extend far inland, into freshwater creeks and rivers. We also show where high rates of mangrove loss intersect with distributions of species that are both listed as threatened by the International Union for the Conservation of Nature (IUCN) and directly associated with mangroves from our literature search (13 species) (D–F). Mangrove loss (2000–2012) was calculated for all 0.2° × 0.2° cells using data from [68], and we show only cells within the top 10th percentile for cells that experienced some loss over this time (i.e., cells with no change or increases were excluded before percentile calculation). See Appendix A for mapping methodology and Appendix E for full global maps in the supplemental information online.

isotope analyses, are providing valuable insight into these associations [7,53]. For example, isotope analysis recently revealed the bonnethead shark as the first truly omnivorous shark, which eats, digests, and assimilates seagrass material [6], an insight that could not have been achieved from telemetry alone. Ultimately, applying combinations of existing and emerging techniques can provide new information that is vital for assessing the vulnerability of coastal ecosystems (and the species within them) to abrupt habitat loss and degradation [54].

We envisage two ways in which new data sets could facilitate updating listings of threatened species to account for loss of and change in coastal wetlands. First, trends in habitats can be incorporated into threat assessments in a qualitative way, so that habitat loss is recognized as a key threatening process in a greater number of assessments. This facilitates conservation agencies to direct species-specific funding toward habitat protection and restoration as a way of preventing extinction. Second, data on the demographic responses of megafauna to wetland loss are needed for models that can be used to quantitatively assess extinction risk. Quantitative assessments are a crucial aspect of prioritizing limited conservation funds between different actions [55], such as habitat protection versus bycatch mitigation, and telemetry data can be used to study behavioural and demographic responses to habitat change, such as changes in mortality (e.g., [26]).

Outstanding Questions

Given that the links between megafauna and vegetated coastal wetlands are more widespread than was known, how can this nexus be used to support protection and restoration of coastal wetlands, and will more accurate information about dependencies help?

How can information on habitat associations within IUCN and other species assessments facilitate on-ground initiatives to conserve and protect coastal wetlands and megafauna?

How do changes in coastal wetlands affect demographic rates and extinction risk of marine megafauna that use wetlands in different ways, such as feeding and reproduction?

Caveats and Limitations

We focused our review on the three major vegetated coastal wetland habitats (seagrasses, mangroves, and saltmarshes) as defined by the Ramsar Convention (see Glossary for Ramsar definition). While other coastal habitats are undoubtedly also important for marine megafauna (e.g., tidal mudflats and inshore coral reefs), we limited our search to these three wetland habitats due to their similarities (conspicuous structural angiosperm vegetation), to ongoing global declines in these habitats, and direct links as diet items for vulnerable marine megafauna taxa. Furthermore, areas of offshore seagrasses do exist. Due to the lack of a strict definition of coastal and the fact that most seagrasses are nearshore, we included all associations with seagrass in our review. Therefore, it is possible that some of the associations identified here come from areas that could be considered non-coastal. Although this means that some species, likely to only be sharks or rays, might not be using strictly coastal seagrasses, their inclusion would not change the conclusions of this review. Even species regarded as truly open ocean, such as the giant manta ray, *Manta birostris,* have been observed swimming over coastal seagrasses in 1.5 m of water [56], highlighting again that associations span a broad continuum of strengths.

Although gray literature can be a useful source of information used in IUCN assessments, we focused on peer-reviewed studies that were able to provide evidence for specific associations, partly under the assumption that a peer-review process is preferred before data should be used to develop hypotheses or incorporated into broader studies. Thus, peer review is a gold standard for quality control of science and a standard for reviews because it provides systematic criteria for searching the literature. Finally, our discussion of the impacts of habitat loss to marine megafauna likely underestimates the magnitude of the problem. For instance, it is likely that a significant number of megafauna not identified here would also be affected by losses in seagrasses, mangroves, or saltmarshes, or the species they support, due to cascading effects on water quality, food webs, and links between coastal wetlands and other habitat types [23,57].

Concluding Remarks and Future Perspectives

Vegetated coastal wetlands are among the most biologically productive ecosystems on earth. Our review identifies key habitat associations between marine megafauna and coastal wetlands, highlighting: (i) the importance of these habitats in the lives and conservation of these species; (ii) the need for greater recognition of habitat change as a potential driver of megafauna decline;

(iii) the need to update and improve IUCN species assessments to align them with current knowledge; (iv) global hotspots of concern where coastal wetland loss and marine megafauna biodiversity intersect (Box 2), and; (v) how existing and emerging techniques can be used in concert to better quantify habitat associations and dependencies.

At present, the importance of coastal habitats to marine megafauna is greatly undervalued, perhaps because there is no review of these habitat associations and low acknowledgment of the importance of vegetated coastal wetlands to megafauna in species assessments. We found that a considerable proportion (13%) of marine megafauna have some link with seagrasses, mangroves, or saltmarshes, with some species exhibiting important, largely obligate habitat associations. Thus, a greater appreciation of the role of these habitats for marine megafauna should be considered when estimating species extinction likelihoods. Our simple yet effective framework for the inclusion of habitat data in IUCN assessments is a starting point for better conceptualizing habitat within assessments. Future research should utilize emerging methods and technologies to strengthen our understanding of the importance of habitat for marine species and aim to quantify levels of habitat dependency rather than just noting associations. We conducted this review to highlight the importance of vegetated coastal wetlands to marine megafauna and spur interest in further describing these associations (see Outstanding Questions), representing a timely advancement towards improving management and conservation outcomes for these important and iconic animals.

Acknowledgments

We thank S. Lopez for mapping and D. Bryan-Brown for providing mangrove loss data. C.J.B., R.M.C., and M.P.T. were supported by a Discovery Project from the Australian Research Council (DP180103124). C.J.B. was supported by a Discovery Early Career Researcher Award (DE160101207) from the Australian Research Council. All authors were supported by The Global Wetlands Project.

Supplemental Information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2019.04.004.

References

1. Bakker, E.S. *et al.* (2016) Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems. *Ecography* 39, 162–179
2. Teh, L.S. *et al.* (2018) An economic approach to marine megafauna conservation in the coral triangle: marine turtles in Sabah, Malaysia. *Mar. Policy* 89, 1–10
3. Randhawa, H.S. *et al.* (2015) Increasing rate of species discovery in sharks coincides with sharp population declines: implications for biodiversity. *Ecography* 38, 96–107
4. Davidson, A.D. *et al.* (2012) Drivers and hotspots of extinction risk in marine mammals. *Proc. Natl. Acad. Sci. U. S. A.* 109, 3395–3400
5. Paleczny, M. *et al.* (2015) Population trend of the world's monitored seabirds, 1950–2010. *PLoS One* 10, e0129342
6. Leigh, S.C. *et al.* (2018) Seagrass digestion by a notorious 'carnivore'. *Proc. R. Soc. Biol. Sci. Ser. B* 285, 20181583
7. Hays, G.C. *et al.* (2016) Key questions in marine megafauna movement ecology. *Trends Ecol. Evol.* 31, 463–475
8. Orth, R.J. *et al.* (2006) A global crisis for seagrass ecosystems. *Bioscience* 56, 987–996
9. Duarte, C.M. *et al.* (2008) The charisma of coastal ecosystems: addressing the imbalance. *Estuar. Coasts* 31, 233–238
10. Davidson, N.C. (2014) How much wetland has the world lost? Long-term and recent trends in global wetland area. *Mar. Freshw. Res.* 65, 934–941
11. Saintilan, N. *et al.* (2014) Mangrove expansion and salt marsh decline at mangrove poleward limits. *Glob. Chang. Biol.* 20, 147–157
12. Foley, M.M. *et al.* (2010) Guiding ecological principles for marine spatial planning. *Mar. Policy* 34, 955–966
13. Sequeira, A.M. *et al.* (2018) Convergence of marine megafauna movement patterns in coastal and open oceans. *Proc. Natl. Acad. Sci. U. S. A.* 115, 3072–3077
14. Doughty, C.E. *et al.* (2016) Global nutrient transport in a world of giants. *Proc. Natl. Acad. Sci. U. S. A.* 113, 868–873
15. Moss, B. (2017) Marine reptiles, birds and mammals and nutrient transfers among the seas and the land: an appraisal of current knowledge. *J. Exp. Mar. Biol. Ecol.* 492, 63–80
16. Bouchard, S.S. and Bjorndal, K.A. (2000) Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology (N. Y.)* 81, 2305–2313
17. Tol, S.J. *et al.* (2017) Long distance biotic dispersal of tropical seagrass seeds by marine mega–herbivores. *Sci. Rep.* 7, 4458
18. Aragones, L.V. *et al.* (2006) Dugong grazing and turtle cropping: grazing optimization in tropical seagrass systems? *Oecologia (Berl.)* 149, 635–647
19. Maxwell, P.S. *et al.* (2017) The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems – a review. *Biol. Rev. (Camb.)* 92, 1521–1538
20. Atwood, T.B. *et al.* (2015) Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Chang.* 5, 1038
21. Ferreira, L.C. *et al.* (2017) The trophic role of a large marine predator, the tiger shark *Galeocerdo cuvier*. *Sci. Rep.* 7, 7641
22. Rodrigues, A.S. *et al.* (2006) The value of the IUCN Red List for conservation. *Trends Ecol. Evol.* 21, 71–76
23. Myers, R.A. *et al.* (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science (Wash. D. C.)* 315, 1846–1850

24. Sheaves, M. (2017) How many fish use mangroves? The 75% rule an ill-defined and poorly validated concept. *Fish Fish. (Oxf.)* 18, 778–789
25. Heupel, M.R. *et al.* (2007) Shark nursery areas: concepts, definition, characterization and assumptions. *Mar. Ecol. Prog. Ser.* 337, 287–297
26. Heupel, M.R. and Simpfendorfer, C.A. (2011) Estuarine nursery areas provide a low-mortality environment for young bull sharks *Carcharhinus leucas*. *Mar. Ecol. Prog. Ser.* 433, 237–244
27. Lee, S.Y. (2004) Relationship between mangrove abundance and tropical prawn production: a re-evaluation. *Mar. Biol. (Berl.)* 145, 943–949
28. Bjorndal, K.A. (2017) Foraging ecology and nutrition of sea turtles. In *The Biology of Sea Turtles* (Vol. I) (Musick, J. and Lutz, P.L., eds), pp. 213–246, CRC Press
29. Marsh, H. *et al.* (2018) Dugongs: seagrass community specialists. In *Seagrasses of Australia* (Larkum, A., ed.), pp. 629–661, Springer
30. Fox, A.G. and Young, R.F. (2012) Foraging interactions between wading birds and strand-feeding bottlenose dolphins (*Tursiops truncatus*) in a coastal salt marsh. *Can. J. Zool.* 90, 744–752
31. Vaudo, J.J. and Heithaus, M.R. (2011) Dietary niche overlap in a nearshore elasmobranch mesopredator community. *Mar. Ecol. Prog. Ser.* 425, 247–260
32. Bethea, D.M. *et al.* (2007) Geographic and ontogenetic variation in the diet and daily ration of the bonnethead shark, *Sphyrna tiburo,* from the eastern Gulf of Mexico. *Mar. Biol. (Berl.)* 152, 1009–1020
33. Morgan, D.L. *et al.* (2015) Discovery of a pupping site and nursery for critically endangered green sawfish *Pristis zijsron*. *J. Fish Biol.* 86, 1658–1663
34. Adulyanukosol, K. *et al.* (2007) Observations of dugong reproductive behavior in Trang Province, Thailand: further evidence of intraspecific variation in dugong behavior. *Mar. Biol.* 151, 1887–1891
35. DeAngelis, B.M. *et al.* (2008) First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. *Mar. Ecol. Prog. Ser.* 358, 257–271
36. Hoffmann, M. *et al.* (2010) The impact of conservation on the status of the world's vertebrates. *Science (Wash. D. C.)* 330, 1503–1509
37. Butchart, S.H. *et al.* (2005) Using Red List Indices to measure progress towards the 2010 target and beyond. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 360, 255–268
38. Newbold, T. *et al.* (2014) A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 281, 20141371
39. Long, A.K. *et al.* (2015) Southern toads alter their behavior in response to red-imported fire ants. *Biol. Invasions* 17, 2179–2186
40. Amorocho, D.F. and Reina, R.D. (2007) Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia. *Endanger. Species Res.* 3, 43–51
41. Gama, L.R. *et al.* (2016) Green turtle *Chelonia mydas* foraging ecology at 25 degrees S in the western Atlantic: evidence to support a feeding model driven by intrinsic and extrinsic variability. *Mar. Ecol. Prog. Ser.* 542, 209–219
42. Guebert-Bartholo, F.M. *et al.* (2011) Using gut contents to assess foraging patterns of juvenile green turtles *Chelonia mydas* in the Paranagua Estuary, Brazil. *Endanger. Species Res.* 13, 131–143
43. Prior, B. *et al.* (2015) Investigating diet and diet switching in green turtles (*Chelonia mydas*). *Aust. J. Zool.* 63, 365–375
44. Ramsar Convention of Wetlands (2018) *Global Wetland Outlook: State of the World's Wetlands and Their Services to People,* Ramsar Convention Secretariat
45. Brown, C.J. *et al.* (2019) The assessment of fishery status depends on fish habitats. *Fish Fish. (Oxf.)* 20, 1–14
46. Magurran, A.E. *et al.* (2010) Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends Ecol. Evol.* 25, 574–582
47. Himes-Cornell, A. *et al.* (2018) Valuing ecosystem services from blue forests: a systematic review of the valuation of salt marshes, sea grass beds and mangrove forests. *Ecosyst. Serv.* 30, 36–48
48. Lee, S.Y. *et al.* (2014) Ecological role and services of tropical mangrove ecosystems: a reassessment. *Glob. Ecol. Biogeogr.* 23, 726–743
49. Corbane, C. *et al.* (2015) Remote sensing for mapping natural habitats and their conservation status – new opportunities and challenges. *Int. J. Appl. Earth Obs. Geoinf.* 37, 7–16
50. He, K.S. *et al.* (2015) Will remote sensing shape the next generation of species distribution models? *Remote Sens. Ecol. Conserv.* 1, 4–18
51. Rose, R.A. *et al.* (2015) Ten ways remote sensing can contribute to conservation. *Conserv. Biol.* 29, 350–359
52. Turner, W. *et al.* (2015) Free and open-access satellite data are key to biodiversity conservation. *Biol. Conserv.* 182, 173–176
53. Pearson, R.M. *et al.* (2017) Realignment of sea turtle isotope studies needed to match conservation priorities. *Mar. Ecol. Prog. Ser.* 583, 259–271
54. Thomson, J.A. *et al.* (2015) Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Glob. Chang. Biol.* 21, 1463–1474
55. Game, E.T. *et al.* (2013) Six common mistakes in conservation priority setting. *Conserv. Biol.* 27, 480–485
56. Adams, D.H. and Amesbury, E. (1998) Occurrence of the manta ray, *Manta birostris*, in the Indian River Lagoon, Florida. *Florida Sci.* 7–9
57. Heck, K.L. *et al.* (2008) Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. *Ecosystems* 11, 1198–1210
58. Scales, K.L. *et al.* (2018) Fisheries bycatch risk to marine megafauna is intensified in Lagrangian coherent structures. *Proc. Natl. Acad. Sci. U. S. A.* 115, 7362–7367
59. Lutcavage, M.E. *et al.* (2017) Human impacts on sea turtle survival. In *The Biology of Sea Turtles* (Vol. I) (Musick, J. and Lutz, P.L., eds), pp. 387–409, CRC Press
60. Law, R.J. (2014) An overview of time trends in organic contaminant concentrations in marine mammals: going up or down? *Mar. Pollut. Bull.* 82, 7–10
61. Sheppard, J.K. *et al.* (2010) Dugong habitat use in relation to seagrass nutrients, tides, and diel cycles. *Mar. Mamm. Sci.* 26, 855–879
62. Hazel, J. and Gyuris, E. (2006) Vessel-related mortality of sea turtles in Queensland, Australia. *Wildl. Res.* 33, 149–154
63. Marsh, H. *et al.* (2011) Ecology and Conservation of the Sirenia: Dugongs and Manatees. Cambridge University Press
64. Bender, D.J. *et al.* (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology (N. Y.)* 79, 517–533
65. Rosencranz, J.A. *et al.* (2018) Sea-level rise, habitat loss, and potential extirpation of a salt marsh specialist bird in urbanized landscapes. *Ecol. Evol.* 8, 8115–8125
66. Chefaoui, R.M. *et al.* (2018) Dramatic loss of seagrass habitat under projected climate change in the Mediterranean Sea. *Glob. Chang. Biol.* 24, 4919–4928
67. Myers, N. *et al.* (2000) Biodiversity hotspots for conservation priorities. *Nature (Lond.)* 403, 853
68. Hamilton, S.E. and Casey, D. (2016) Creation of a high spatio-temporal resolution global database of continuous mangrove forest cover for the 21st century (CGMFC-21). *Glob. Ecol. Biogeogr.* 25, 729–738
69. Richards, D.R. and Friess, D.A. (2016) Rates and drivers of mangrove deforestation in Southeast Asia, 2000–2012. *Proc. Natl. Acad. Sci. U. S. A.* 113, 344–349
70. Ramsar Convention Secretariat (2016) *The Fourth Ramsar Strategic Plan 2016–2024. Ramsar Handbooks for the Wise Use of Wetlands* (Vol. 2, 5th edn), Ramsar Convention Secretariat