Hydrobiologia

A Review of seagrass ecosystem services: Providing nature-based solutions for a changing world

--Manuscript Draft--

Manuscript Number:	HYDR-D-22-00247R5
Full Title:	A Review of seagrass ecosystem services: Providing nature-based solutions for a changing world
Article Type:	Review paper
Keywords:	Seagrass; Ecosystem services; Conservation; nature-based solutions.
Corresponding Author:	Mariana do Amaral Camara Lima, Ph.D. University of Salford UNITED KINGDOM
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	University of Salford
Corresponding Author's Secondary Institution:	
First Author:	Mariana do Amaral Camara Lima, Ph.D.
First Author Secondary Information:	
Order of Authors:	Mariana do Amaral Camara Lima, Ph.D.
	Thaisa Fernandes Bergamo, PhD
	Raymond Ward
	Chris Joyce
Order of Authors Secondary Information:	
Funding Information:	
Abstract:	Seagrasses are marine flowering plants, which form extensive meadows in intertidal and shallow-water marine environments. They provide a range of ecosystem services, which directly or indirectly benefit humans, grouped into four broad categories: provisioning (e.g., food production); regulating (e.g., carbon sequestration); supporting (e.g., primary production); and cultural (e.g., recreational). This study reviews publications focusing on seagrass ecosystem services provision, to identify knowledge gaps and improve our understanding of the use of these habitats as nature-based solutions to societal challenges, such as climate change. Results showed that some ecosystem services, namely food provision, carbon sequestration and maintenance of biodiversity/nursery habitats receive a higher level of focus and attention than others, such as regulation of diseases and social relations, which are rarely included in studies. It is clear that to fully comprehend the nature-based solution potential of seagrass ecosystems, ecosystem services need to be considered as a whole, and results need to be shared across global regions, to understand the potential impacts of degradation and loss of these ecosystems. Suggestions include applying novel technologies such as remote sensing and ecological niche modelling to address some of the gaps in seagrass research, and incorporate preservation of seagrass ecosystems in marine management plans.
Response to Reviewers:	All changes required have been addressed.

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Authors: Mariana do Amaral Camara Lima[1]; Thaisa F. Bergamo[2,3]; Raymond D. Ward[2,4] and Chris B. Joyce[4]

Corresponding author: M.doamaralcamaralima@salford.ac.uk

Institutions:

1 – School of Science, Engineering & Environment - University of Salford, Manchester M5 4WT, England U.K.

2- Institute of Agriculture and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 13 5, 51014 Tartu, Estonia.

3 - Department of Geographical and Historical Studies, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland.

4 - Centre for Aquatic Environments - School of the Environment and Technology, University of Brighton - Brighton BN2 4GJ, England, U.K.

Statements and Declarations

Competing Interests: None

Funding: The authors did not receive support from any organization for the submitted work.

Employment: Present for all authors

Financial interests: The authors declare they have no financial interests.

Non-financial interests: none

Data availability: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability: Not Applicable

Author contributions: All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by [Mariana Lima], [Thaisa Bergamo], [Raymond Ward] and [Christopher Joyce]. The first draft of the manuscript was written by [Mariana Lima] and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Acknowledgments

We would like to kindly thank the reviewers for the time spent reading and evaluating our manuscript

Abstract

Seagrasses are marine flowering plants, which form extensive meadows in intertidal and shallow-water marine environments. They provide a wide range of ecosystem services, which directly or indirectly benefit humans, and can be grouped into four broad categories: provisioning (e.g., food production); regulating (e.g., carbon sequestration); supporting (e.g., primary production); and cultural (e.g., recreational, and eco-tourism). This study provides a review of publications focusing on seagrass ecosystem services provision, to identify knowledge gaps and improve our understanding of the use of these habitats as nature-based solutions to societal challenges, such as climate change. Results showed that some ecosystem services, namely food provision, carbon sequestration and maintenance of biodiversity/nursery habitats receive a higher level of focus and attention than others, such as regulation of diseases and social relations, which are rarely, if ever, included in studies. It is clear that in order to fully comprehend the nature-based solution potential held by seagrass ecosystems, studies need to consider ecosystem services as a whole, and also combine and share results across global regions, to better understand the potential impacts of degradation and loss of these ecosystems worldwide. Suggestions include applying novel technologies such as remote sensing and ecological niche modelling to address some of the main gaps in seagrass research, like meadow extent and connectivity within landscapes, to better incorporate preservation of seagrass ecosystems in marine management plans.

Keywords: Seagrass, ecosystem services, conservation, nature-based solutions.

Introduction

Marine and coastal ecosystems and their related economic and social services have been suffering profound impacts due to human induced climate change (IPCC, 2018). Thus, a better understanding of how these ecosystems function, the services they provide (in both ecological and economic terms), and what is at stake should we lose them, are necessary parts of any coastal management plan (Fisher *et al*., 2009; Heckwolf *et al*., 2021). Vegetated coastal systems characterise ecologically important areas where the land meets sea and are generally composed of plant species adapted to either fully or partially submerged environments (Short *et al*., 2016). These systems are home to a wide range of ecological and economic activities (Royal Society, 2017), and provide numerous ecosystem services, including the provision of nursery habitats for commercially important marine species, raw materials, coastal protection, and enhancing water quality (Lau, 2013). Vegetated coastal systems are sometimes referred to as "blue carbon" ecosystems due to their role as carbon sinks (Mcleod *et al*., 2011; Pendleton *et al*., 2012). Thus, by capturing and sequestering carbon from the atmosphere, these blue carbon ecosystems play an important role in climate change mitigation (Fourqurean *et al*., 2012; Veettil *et al*. 2018; Lima *et al*. 2020; Ward, 2020).

Coastal ecosystems, when in pristine condition, naturally provide diverse benefits to both humans and nature. Therefore, effective nature conservation strategies are necessary to guarantee their continued or enhanced ecosystem service provision (Watson & Zakri, 2003; Rigo *et al*., 2021). The Millennium Ecosystem Assessment

(2005) uses a broad definition that equates 'the benefits people obtain from ecosystems' with the term 'ecosystem services.' As per the definition by the Millennium Ecosystem Assessment Board, 'an ecosystem is a dynamic complex of plant, animal, and microorganism communities and the non-living environment, interacting as a functional unit', including humans as an integral part of many ecosystems (Watson & Zakri, 2003). Amongst vegetated coastal systems, seagrass meadows have been identified as important ecosystem service providers, especially as there is strong evidence that healthy seagrass beds enhance the productivity of neighbouring systems like mangroves, salt marshes and coral reefs (de los Santos *et al*., 2020; Cziesielsk *et al*., 2021).

Seagrasses

Seagrass meadows have a pan-global distribution, being found in shallow coastal areas of all continents, except Antarctica (Garrard and Beaumont, 2014). Seagrasses occupy soft-bottom sediments of the world's oceans from the tropics to the temperate zones (World Resources Institute, 2005), extending from the intertidal zone to depths of up to 40 m (Gutiérrez *et al*. 2011). There is a high variation in the estimated global areal coverage of seagrass meadows, ranging from 17 x 10^6 to 60 x 10^6 ha worldwide (Hemminga & Duarte, 2000; Mcleod *et al*. 2011). This uncertainty highlights the need for more research, to better map and understand seagrass global distribution, including seasonal and long-term temporal variations (Garrard and Beaumont, 2014; Macreadie *et al*., 2018).

Seagrasses are marine angiosperms (**Figure 1**) adapted to exist fully submerged in brackish or salt water, where they promote sediment deposition, stabilise substrates, decrease water velocity and function as part of the estuarine filtration system, removing contaminants from the water column (Orth *et al*., 2006; Campagne *et al*., 2015). Seagrasses also provide a range of other ecosystem services to the marine environment, including nutrient cycling, supporting a range of commercially important fish species as a nursery habitat and as an important food source for mega-herbivores such as green turtles, dugongs, and manatees (Costanza *et al*., 1997; Hemminga & Duarte 2000; Orth *et al*., 2006; Björk *et al.,* 2008; Nordlund *et al*., 2018; de los Santos *et al*., 2020).

Seagrasses can also act as ecological engineers, altering their environment to improve conditions by reducing suspended sediment concentrations, which can increase light availability and reduce water column pollutant levels, resulting in improved conditions for seagrass growth and survival as well as other marine photosynthetic organisms (van der Heide *et al*., 2007 Paquier *et al*., 2014; Serrano *et al*., 2016). Seagrass canopies can also reduce wave attenuation, and this combined with a dense root matrix can further promote sediment deposition and prevent erosion (Potouroglou *et al*., 2017). Some species, particularly those with high canopy density and above ground biomass have been shown to reduce current velocities by up to 90%, resulting in net sediment accretion rates of up to 2 mm $year^{-1}$ (Hogarth, 2015).

Therefore, seagrasses directly and indirectly provide a range of ecosystem services, which vary by geographical region and genera (Cullen-Unsworth *et al*., 2014; Nordlund *et al*., 2016; Nordlund *et al*., 2018). The diversity of ecosystem services is categorised as provisioning (ecological goods, such as food, fisheries, etc. provided directly by seagrasses or indirectly by associated species), regulation and maintenance (ecological services, such as climate regulation, water filtration, and ecological processes), supporting (primary production, soil formation) and cultural (spiritual or knowledge values, such as recreation, tourism, and education) (Campagne *et al*., 2015; Nordlund *et al*., 2016).

Nature-Based Solutions

Nature-based solutions (NbS) are defined as innovations inspired and supported by nature, which provide environmental, social, and economic benefits, and help build resilience by benefiting biodiversity and supporting the delivery of a range of ecosystem services (Seddon, *et al*., 2019; Wild *et al*., 2020; UNEP, 2020). NbS can address such current and vital societal challenges as climate change and associated impacts, environmental pollution, food security and water scarcity. NbS include established approaches such as ecosystem-based adaptation, ecosystem-based disaster risk reduction, green and blue natural infrastructure, as well as the more recently described "natural climate solutions" (Cohen-Shacham *et al*., 2016, 2019; Griscom *et al*., 2017; Chausson *et al*., 2020).

The potential of seagrass ecosystems as NbS, including climate mitigation, is evidenced through the high carbon sequestration and storage potential, which could be used for CO_2 offsets in nationally determined contributions, particularly in the case of successful restoration (Stankovic *et al*., 2021; Lima *et al*., 2022). Stankovic et al. (2021) suggest that successful and well-designed restoration projects and conservation measures, could result in seagrass meadows contributing up to 1.43% towards CO_2 offset of countries' total emissions by 2030 (business-as-usual, BAU scenario). However, the climate solution potential of seagrasses is still one of the most poorly represented as a NbS (Chausson *et al*., 2020; UNEP, 2020; Veettil *et al*. 2021), partly because seagrass meadows are especially vulnerable to anthropogenic impacts from both adjacent terrestrial and marine systems (Unsworth *et al*., 2019). Such impacts can be physical, resulting in direct removal of plants, or chemical, polluting both the sediment and water (Mazarrasa *et al*., 2017). Moreover, storms and severe weather events, associated with climate change, can affect seagrass populations by uprooting plants and mobilizing sediments, increasing turbidity, and reducing water quality and light penetration (Cardoso *et al*., 2008). Additionally, fluctuations in sea temperature are considered the primary climate change related threat to seagrass ecosystems, which could lead to alterations in seagrass distribution and metabolism, subsequently reducing net autochthonous carbon sequestration potential (Clausen *et al*., 2014; Hyndes *et al*., 2016; Mazarrasa *et al*., 2018). Furthermore, sea level rise may alter habitat availability for intertidal seagrass species, and as projected by the IPCC (2019) with medium confidence under the RCP8.5 emission scenario by the end of the century, vegetated coastal ecosystems in general are at high risk of local losses.

Past studies estimate the value of coastal ecosystem services to be US$31.6 tr yr^{-1} covering seagrass meadows and algae beds as well as tidal marshes and mangroves (Bertram *et al*., 2021). However, compared to other coastal ecosystems (such as mangroves and corals) that also benefit humans, there has been substantially less research focus on identifying and valuing ecosystem services provided by seagrasses, mainly due to the absence of detailed information on marine habitat distribution and the difficulties in assessing both processes and functions (Maes *et al*., 2012; Himes-Cornell *et al*., 2018). Consequently, the value of seagrasses as an ecosystem is often not considered in marine management decisions, and rarely incorporated into NbS projects (Duarte *et al*., 2008; Grech *et al*., 2012; Chausson, *et al*., 2020). In addition, non-monetary values of seagrasses are important, with some studies assessing non-monetary values by using biological proxies, such as area coverage, the biomass of bird and mammal groups that seagrass supports, or the energy resources invested by nature when estimating the benefits of seagrass as a habitat (Plummer *et al*., 2013; Vassallo *et al*., 2013).

The lack of public awareness concerning the importance of the ecosystem services that seagrasses provide is arguably one the biggest threats to their conservation. This suggests that studies highlighting the importance of ecosystem service provision by seagrasses can raise the profile of this important habitat and provide support for their protection and conservation (Nordlund *et al*., 2018; Quevedo *et al*., 2020). Thus, this research evaluates and lists the services provided by seagrass ecosystems by conducting a comprehensive review of the literature, in order to identify potential gaps in knowledge and areas of focus or concern for the future. The aim of this review is to contribute to a better understanding of how seagrass ecosystem services have been studied so far, with the goal of constructing a knowledge-base for future NbS projects. The objective of this study is to review how the main ecosystem services provided by seagrass meadows have been reported over time to highlight the need for protection and preservation of their natural assets, in order to successfully develop NbS that incorporates these extremely productive ecosystems.

Methods

Literature Search

A systematic literature review was conducted in order to better understand the range of studies that have been published to assess the ecosystem services provided by seagrasses. The search centred on studies explicitly focused on ecosystem services (**Figure 2**). The literature search was conducted using the Web of Science scientific citation database. The studies were searched in the Web of Science Core collection (editions: Science Citation Index Expanded, Social Sciences Citation, Conference Proceedings Citation, Emerging Sources Citation, Conference Proceedings, Citation – Social Science & Humanities and Book Citation Science) considering the period between 1900 and March 2022, using the following search string applied to all fields: (seagrass*⁄ OR "sea grass*/") AND ("ecosystem⁄ service*⁄"), resulting in a total of 684 papers. A second search was conducted using the same search string but applied to the field topic (title (title, key words, and abstract), resulting in a total of 654 papers.

For the purpose of this study, the search focused on peer reviewed papers, excluding grey literature. It is likely that some of the literature on ecosystem services provided by seagrasses may have been published as working papers, government reports, or other additional grey literature sources. However, it is not feasible to develop search criteria that will identify all such possible studies within the topic of this study. Moreover, there are likely additional publications on studies for ecosystem services in seagrass habitats that do not mention the specific key words included in our search criteria.

Selection Criteria

In order to select articles to include in this review, all 684 publications were screened. Only publications that mentioned seagrass ecosystem services in the title, abstract or key words, or if the content was unclear reading the abstract, were retained, yielding 654 publications. Through this selection, the publications retained from the Science Citation Index Expanded were used for full-text reading and analysis. After full text reading, 105 publications (16% of all screened publications) were retained that focused on the description, valuation, or inclusion of one or more ecosystem services provided by seagrasses as the main topic of research, even if this was integrated into analyses with other coastal habitats such as, mangroves, salt marshes or coral reefs.

Data extraction

For those final selected publications, the publication year; type of publication; the ecosystems services discussed; the geographic area where the study was conducted; and the threats to the studied ecosystems were extracted. Ecosystem services were organised into categories based on the classification scheme defined by the Millennium Ecosystem Assessment (2005). The Millennium Ecosystem Assessment was chosen as a framework for this study as it was conducted as a multiscale assessment, with interlinked assessments undertaken at local, national, regional, and global scales, incorporating seagrass ecosystem services within their Marine, Coastal, and Island Systems section.

Results

Overall, there has been an annual increase in the number of studies including evaluation of seagrass ecosystem services, over the 23 years under study, with 19% (n=20) of the cumulative total of studies being published in 2021 (**Figure 3**). Studies ranged from reviews of existing ecosystem services, assessment of current threats, evaluation of public or stakeholders' perspectives, and knowledge gaps, to models for assessing ecosystem services and valuation.

Of the 105 studies analysed, 37% (n=39) had a global approach to seagrass ecosystem services, 34% (n=36) focused on specific global regions, mainly meadows in the Caribbean (n=5), Africa (n=5), and the Mediterranean (n=3), and 42 studies analysed seagrass ecosystem services at national level, representing 40% of the total number. The most prolific nations studied were the USA (n=9) and Spain (n=8), followed by Australia with 4 studies and Sweden and the UK, both with 3 studies each (**Table S1**). Approximately half of the analysed studies focused solely on ecosystem services provided by seagrasses (n=55), while the other half provided a combined approach, grouping seagrasses with other blue carbon ecosystems such as mangroves, coastal wetlands, kelp forests and coral reefs. Out of the 55 studies focussing on seagrass, 17 (16% of the total) concentrated on *Posidonia oceanica* (Linnaeus, 1813) meadows specifically. It was also noted that more recent studies focused exclusively on ecosystem services provided by seagrass habitats, whilst older ones usually combined seagrasses within wetlands and/or other coastal habitats such as oyster and coral reefs (**Table S1**).

Most studies described threats to seagrasses and their related ecosystem services. Although studies reported those threats differently, the nomination of threats provides an insight into the potential for changes in the area of intact seagrass ecosystems as well as challenges that resource managers likely face within each region, such as to fisheries. Within the studies evaluated, the greatest emphasis was placed on threats associated with land conversion, pollution, climate change, aquaculture, and unsustainable resource use (**Table S1**). The most cited threats in these studies have also been highlighted by the general literature on seagrass ecosystems, namely climate change, sea level rise, pollution, fishing, and urbanisation (Unsworth *et al*., 2019; Young *et al*., 2021; Moksnes *et al*., 2021).

Altogether, ecosystem services were reported 396 times within the selected studies, and these have been classified into types relating to provisioning, regulating, supporting and cultural services (**Table 1, Figure 4**). Although the wider literature regularly cites the large number of ecosystem services and benefits provided by seagrass systems, these are not always the central focus of research, rather being used as a means to justify the importance of studying these habitats. It has also been noted that a subset of ecosystem services tends to be researched much more frequently than others (**Figure 4**). For example, researchers tend to focus on carbon sequestration (n= 60), food provision (n= 49 studies), maintenance of habitat and biodiversity/nursery habitats (n= 37), storm protection/extreme events (n= 31) and opportunities for recreation and tourism (n= 29) far more than any of the other seagrass ecosystem services (**Table 1**). In addition, regulating services overall tend to be studied much more frequently than other categories of ecosystem services, representing 42% of the total with 166 mentions, whilst the least explored were provisioning services with 17% of total reports (n=66) (**Table 1; Figure 4**). Moreover, some seagrass ecosystem services identified by the Millennium Ecosystem Assessment are rarely, or sometimes never, assessed including, provisioning services of fuel or fresh water (**Table 1**).

In total, 17 studies provided valuation models for the ecosystem services described (**Table S1**). Services such as food security and raw material provisioning, and opportunities for recreation and tourism have mainly been assessed and used to value the ecosystem service provided by seagrass habitats. Researchers have used market prices to measure food, raw material, climate regulation (via carbon sequestration), and opportunities for recreation and tourism, while voided cost and replacement cost are generally used to value waste treatment and moderation of extreme events.

Discussion

Although the need to study ecosystem services for seagrasses is indicated by the increasing number of publications, findings are mostly focused on seagrass cover and distribution mapping (Hossain *et al*., 2014; Nordlund *et al*., 2016; Nordlund *et al*., 2018) except a few species-specific case studies focusing mainly on *Posidonia* spp. (Vassallo *et al.*, 2013; Campagne *et al*., 2015). Moreover, this review demonstrates that some ecosystem services are studied much more frequently than others (e.g., food provision in 47% of studies, carbon sequestration in 57% of studies), likely because of stakeholder interest and current climate change mitigation policies. Several important services are poorly addressed (i.e., medicinal, and genetic resources, air quality, regulation of water flow, biological control, spiritual experience) or entirely absent (i.e., fuel, ornamental resources, inspiration for culture/art) in the literature, most likely due to poor data availability and the difficulty of quantifying the extent of service provision. However, although this systematic review followed established search protocols, it limited the search to the wider term 'seagrass ecosystem services' within titles, key words or abstracts, which restricts the analyses of studies where seagrass ecosystem services do not feature in those sections, even though they might be indirectly evaluated or quantified in other sections. Consequently, for example, few studies from the UK were included in the search, although researchers such as Lima *et al*., (2020, 2022), Potouroglou *et al*., (2021), Green *et al*., (2018) and others have been assessing the UK's seagrass carbon stocks with the aim of promoting natural climate solutions. Another limitation to consider is that this review focused on scientific journal publications only, which discards regional and global reports on the assessment of seagrasses' ecosystem services and their potential as NbS, e.g. UNEP (2020). Nevertheless, this review suggests that there has been an increase in the inclusion of the term 'ecosystem services' in seagrass studies in more recent years, showing a positive trend of raising awareness of their importance as NbS.

Seagrass carbon stock analyses have been reported worldwide, even though there might be a bias of reported global estimates, which mainly focus on values from tropical and Mediterranean seagrass meadows dominated by larger species, like *Posidonia* spp. (Johannessen and Macdonald, 2016; Serrano et al., 2018; Lima et al., 2022). Although this demonstrates that many studies have been focusing on seagrasses' potential as NbS for climate change mitigation, these are not always evidenced as an ecosystem service provision, and even more rarely linked to the categories proposed by the Millennium Assessment, as described in this study. Therefore, despite a broad recognition of the importance of such data (Pascual *et al*., 2017), serious gaps in the identification of ecosystem services provided by seagrass ecosystems still exist, notably involving methodology, areal extent, and valuation of ecosystem services (Nordlund *et al*., 2018; de los Santos *et al*., 2020). The variability of ecosystem services across a seascape, including spatial (i.e. extent of a seagrass meadow and its ability to buffer storm waves) and temporal differences (seasonal fluctuations and density of seagrass biomass) may influence the assessment and quantification of some services and should be considered by researchers and policymakers (Barbier *et al*., 2011).

Mapping the services provided by seagrass ecosystems is key to evaluating temporal and spatial alterations to their provision, particularly when taking a regional approach, such as those reviewed in this study for the Caribbean and Mediterranean (de los Santos *et al*., 2020). Mapping ecosystem services is one of the requirements in ecosystem accounting, tracking alterations in natural assets and evaluating links with economic and human activities (Veettil *et al*., 2020). Despite advances in seagrass ecosystem service assessment studies and extent mapping, there are still large global and regional data gaps (Veettil *et al*., 2020; 2022), predominantly as a result of the in situ approaches that are typically used including scuba/snorkeling surveys (Gotceitas *et al*., 1997), ground-based sampling (Moore *et al*., 2000), and hovercraft-based mapping (McKenzie, 2003).

Even though projects focused on the protection and sustainable management of vegetated coastal environments, including seagrass, are not a novelty, such efforts are mainly aimed at generating benefits and services to local communities and biodiversity, as well as the fisheries and tourism sectors (Herr *et al.*, 2014; Mitsch and Mander, 2018). Unlike terrestrial ecosystems, few coastal programs have been established with the goal of conserving and restoring ecosystems as potential mechanisms for nature-based climate mitigation (carbon capture/ avoided emissions) solutions (Herr *et al.*, 2011; Gattuso *et al*., 2018). Chausson *et al*., (2020) assessed the six most represented ecosystem types when examining the effectiveness of nature-based interventions to address climate impacts and emphasised that only 13% of studies included coastal ecosystems, with only one study, out of 386, focused on seagrass ecosystems specifically. Herr and Landis (2016) highlight that even though 151 countries contain at least one blue carbon ecosystem (seagrass, mangrove, or saltmarsh) with 71 containing all three, only 28 countries include references to vegetated coastal systems in terms of climate crisis mitigation in their intended nationally determined contributions (INDCs). Hence, undertaking ecosystem service assessments, such as those presented in this review, could provide key data to identify conservation and management actions for these ecosystems to be incorporated in such strategies (Pabon-Zamora *et al*., 2008; Pascual *et al*., 2017).

Half of the studies in this review focused on seagrass meadows specifically while the other half incorporated neighbouring ecosystems in their ecosystem services appraisal. It has been reported that in order to comprehensively assess ecosystem services, it is necessary to incorporate the multiple and synergistic characteristics of ecosystems (Koch *et al*., 2009; Barbier, 2012). However, studies continue to focus on each service independently, even though ecological interactions suggest that there is connectivity between vegetated coastal ecosystems, which impacts the availability and/or quality of the services (Barbier *et al*., 2011). By assessing ecosystem services collectively, like some of the papers in this review, studies could better delineate between functions, services, and benefits to avoid the problem of double counting that may arise due to the fact that some services (i.e., supporting and regulating) provide the basis and inputs for the assessment of others (Boyd & Banzhaf, 2007; Fisher *et al*., 2009; Kumar, 2012). For example, in recent years, ecological niche modelling has been used as an alternative tool to predict the effects of climate change on seagrass ecosystem distributions (Valle *et al*., 2014; Davis *et al*., 2016; Chefaoui *et al*., 2018), the potential distributions of certain seagrass-associated species (March *et al*., 2013; Chefaoui *et al*., 2016; Jayathilake & Costello, 2018) and seagrass conservation priorities (Valle *et al*., 2013; Adams *et al*., 2016). Ecological modelling can be a useful and promising tool for seagrass restoration programs, as it is used to determine the most favourable environmental conditions for species growth by collecting large scale datasets for seagrass meadows, including variables such as: light intensity; seagrass coverage and biomass; sediment accretion rates; water velocity; sediment parameters and porewater nutrients (Valle *et al*., 2011; Adams *et al*., 2016; Stankovic *et al*., 2019; Horn *et al*., 2021).

To effectively include seagrass ecosystems in climate regulation policy, a comprehensive understanding of the factors that control carbon stocks, and sequestration rates, are urgently required (Lima *et al*., 2020). The reported loss of seagrasses capacity to sequester and store carbon is of high concern, highlighting the need for protection and conservation of these ecosystems (Unsworth *et al*., 2018). This should be undertaken to not only maintain the carbon stored in their sediments, but also to maintain important supporting ecosystem services linked to biodiversity, such as: critical feeding grounds for birds; important nursery areas for seabass; supporting threatened runs of migratory salmon and sea trout on their way to and from spawning grounds, as well as migration routes for eels to spawn at sea (Jackson *et al*., 2001; Hiscock *et al*., 2005; Lilley & Unsworth, 2014; Harding *et al*., 2016; Jones *et al*., 2018; Bertelli & Unsworth, 2018; de los Santos *et al*., 2020). To date, conservation programs are rarely based on the explicit consideration of threats and drivers for a specific seagrass meadow, and instead focus on conserving seagrass as part of a broader management plan incorporating other habitats or species, like many reviewed by this study (Jones *et al*., 2018). One way to improve this and highlight their importance would be to include conservation and protection of seagrass ecosystems in financing mechanisms involving the reduction of CO_2 emissions as a natural climate mitigation solution (Wylie *et al*., 2016; Herr *et al*., 2017; Howard *et al*., 2017; Barbier *et al*., 2018; Himes-Cornell *et al*., 2018).

Some seagrass areas have been reported to rival coral reefs in terms of supporting biodiversity, and when associated with adjacent mangrove and barrier reef systems, they can provide more protection services than the corals themselves and compensate for long term degradation of the reefs (Guannel *et al*., 2016). The indirect value of the supporting services provided by seagrasses, including providing shelter and nutrition to a range of marine species, adds to their wider ecological importance (Hogarth, 2015; Nordlund *et al*., 2016; Nordlund *et al*., 2018). However, many ecosystem services provided by seagrasses remain poorly studied, or not clearly referenced, especially indirect use values and non-use values (Himes- Cornell *et al*. 2018). With the recent focus on the climate mitigation potential of blue carbon ecosystems in the realm of international conservation (e.g., the Paris Agreement, UN SDG 14), coastal managers would benefit from a better understanding of the valuation of services provided by seagrass ecosystems. Jones and Unsworth (2016), further note that there are a wide range of risks associated with poor environmental management of seagrass meadows, particularly concerning the provisioning service of food security, the most frequent service described in this review, given their value as fisheries nursery habitats.

As a consequence of their sensitivity to disturbance and broad geographical range, seagrasses are considered to be excellent biological indicators to be included in intended nationally determined contributions (INDCs) as NbS (Pergent et al., 2015; UNEP, 2020). NbS are increasingly recognised as vital to achieving climate mitigation and conservation targets, with seagrass meadows in the UK and northern Europe, for example, being typically included in conservation law and agendas, either directly or indirectly (Harding *et al*., 2016; Jackson *et al*., 2016). However, studies suggest that these programs might not have been effective in protecting these ecosystems, with declines being consistently reported (Jones and Unsworth, 2016; Jones *et al*., 2018; Smale *et al*., 2019). Also, NbS, including seagrass restoration, are not typically among the lowest cost options and so do not form a major proportion of compliance markets, aimed to meet greenhouse gas emissions and climate change legislation (UNEP, 2020). Conversely, NbS are popularly represented in voluntary markets, with several methods being developed for seagrass restoration, including through the Verified Carbon Standard (Needelman *et al*., 2018; UNEP, 2020).

Conclusions

Following the publication of the Millennium Ecosystem Assessment (MEA, 2005) and the Economics of Ecosystems and Biodiversity report (Kumar, 2012), there has been increased interest in the development of national, regional, and global ecosystem services indicators. However, the full range of ecosystem services provided by seagrass ecosystems has not been appropriately quantified, suggesting that informed management decisions cannot be formulated. An increase in the geographic coverage of ecosystem services studies is recommended, especially in understudied areas such as Africa, South America and the Middle East, in order to improve value estimates by region and meadow type. Regional/global-scale datasets of spatially explicit seagrass species presence-absence, abundance, and estimates of their ecosystem service provision, although currently lacking, could support resource management, and facilitate global conservation targets demanded by multilateral environmental agreements, policies, and initiatives, especially those including natural climate solutions. Thus, future research needs to focus on: 1) incorporating less studied ecosystem services, especially those related to social relations and cultural heritage into valuation studies to fully grasp the natural capital provided by the seagrass ecosystem; 2) incorporating remote sensing techniques to better map seagrass meadows' areal extent and variability among species and sites, to better identify regions where losses of ecosystem services may be occurring; 3) use of ecological niche modelling as an ecosystem based management tool to better understand seagrass ecology and connectivity with other coastal habitats; 4) improved communication between regions and across disciplines, especially those that focus on ecosystem services provided by other coastal vegetated ecosystems adjacent to seagrass meadows, like salt marshes, mangroves, macroalgae and coral reefs. Results from this study showed a growing interest in researching ecosystem services provided by seagrass meadows, and also highlighted the threats hindering the provision of these services. Thus, more needs to be done, as detailed above, to make sure that the full scope of ecosystem services are recognised and appropriately assessed, to be effectively included in marine coastal management planning as NbS.

Reference List

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Table 1: Integrated heat map representing the frequency of studies that developed seagrass ecosystem service valuation estimates for each ecosystem service category between 2000 and March 2022, per the Millennium Ecosystem Assessment Board classification scheme, (2005). Values of 0 represent no studies published for a particular ecosystem service that year.

		2000	2003	2004	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	Total
Provisioning Services	Food and fibre	1	0	1	0	1	0	0	1	3	0	2	6	4	3	2	4	3	5	9	4	49
	Fuel	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2
	Genetic resources	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	5
	Biochemicals / Fertilisers	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	1	0	3	1	9
	Ornamental resources	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	Fresh water	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Regulating Services	Air quality maintenance	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	2	0	7
	Carbon Sequestration	1	0	0	1	0	0	0	0	4	2	3	2	6	5	1	6	5	5	15	4	60
	Water regulation	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2	1	5
	Erosion control	1	1	0	0	1	0	1	0	1	0	0	2	4	3	1	0	1	1	5	1	23
	Water purification	0	0	0	0	0	0	0	0	1	0	0	1	3	2	1	2	1	3	6	2	22
	Waste treatment	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	3
	Disease regulation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
	Biological control	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	4
	Pollination	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Storm protection	0	0	0	0	1	1	0	0	2	0	1	0	3	5	1	4	2	4	6	1	31
	Climate regulation	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	6	0	9
Supporting Services	Soil formation	1	1	0	0	0	0	0	0	0	0	2	0	1	2	1	1	2	0	3	0	14
	Nutrient cycling	1	0	0	0	0	0	1	1	2	1	1	1	3	1	0	3	0	1	3	0	19
	Primary production	1	0	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	1	3	1	10
	Maintanance of biodiversity/Habitat	0	0	1	0	0	0	0	1	1	0	1	2	4	2	3	2	3	4	10	3	37
Cultural Services	Cultural diversity	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	5
	Spiritual and religious	0	0	0	0	0	0	0	0	0	0	1	2	1	1	0	1	1	0	1	0	8
	Knowledge systems	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	1	0	6
	Educational	1	0	0	0	0	0	0	0	0	0	1	1	2	1	0	0	2	0	4	0	12
	Inspiration	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	3
	Aesthetic	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	1	0	1	1	7
	Social relations	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2
	Sense of place	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2
	Cultural heritage	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	2	1	10
	Recreational and ecotourism	1	0	0	0	0	0	0	0	1	0	1	2	7	3	0	2	2	3	5	2	29

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Title: A Review of seagrass ecosystem services: Providing nature-based solutions for a changing world

Authors: Mariana do Amaral Camara Lima[1]; Thaisa F. Bergamo[2,3]; Raymond D. Ward[2,4] and Chris B. Joyce[4]

Corresponding author: M.doamaralcamaralima@salford.ac.uk

Institutions:

1 – School of Science, Engineering & Environment - University of Salford, Manchester M5 4WT, England U.K.

2- Institute of Agriculture and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 13 5, 51014 Tartu, Estonia.

3 - Department of Geographical and Historical Studies, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland.

4 - Centre for Aquatic Environments - School of the Environment and Technology, University of Brighton - Brighton BN2 4GJ, England, U.K.

Statements and Declarations

Competing Interests: None

Funding: The authors did not receive support from any organization for the submitted work.

Employment: Present for all authors

Financial interests: The authors declare they have no financial interests.

Non-financial interests: none

Data availability: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability: Not Applicable

Author contributions: All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by [Mariana Lima], [Thaisa Bergamo], [Raymond Ward] and [Christopher Joyce]. The first draft of the manuscript was written by [Mariana Lima] and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Acknowledgments

We would like to kindly thank the reviewers for the time spent reading and evaluating our manuscript

Abstract

Seagrasses are marine flowering plants, which form extensive meadows in intertidal and shallow-water marine environments. They provide a wide range of ecosystem services, which directly or indirectly benefit humans, and can be grouped into four broad categories: provisioning (e.g., food production); regulating (e.g., carbon sequestration); supporting (e.g., primary production); and cultural (e.g., recreational, and eco-tourism). This study provides a review of publications focusing on seagrass ecosystem services provision, to identify knowledge gaps and improve our understanding of the use of these habitats as nature-based solutions to societal challenges, such as climate change. Results showed that some ecosystem services, namely food provision, carbon sequestration and maintenance of biodiversity/nursery habitats receive a higher level of focus and attention than others, such as regulation of diseases and social relations, which are rarely, if ever, included in studies. It is clear that in order to fully comprehend the nature-based solution potential held by seagrass ecosystems, studies need to consider ecosystem services as a whole, and also combine and share results across global regions, to better understand the potential impacts of degradation and loss of these ecosystems worldwide. Suggestions include applying novel technologies such as remote sensing and ecological niche modelling to address some of the main gaps in seagrass research, like meadow extent and connectivity within landscapes, to better incorporate preservation of seagrass ecosystems in marine management plans.

Keywords: Seagrass, ecosystem services, conservation, nature-based solutions.

Introduction

Marine and coastal ecosystems and their related economic and social services have been suffering profound impacts due to human induced climate change (IPCC, 2018). Thus, a better understanding of how these ecosystems function, the services they provide (in both ecological and economic terms), and what is at stake should we lose them, are necessary parts of any coastal management plan (Fisher *et al*., 2009; Heckwolf *et al*., 2021). Vegetated coastal systems characterise ecologically important areas where the land meets sea and are generally composed of plant species adapted to either fully or partially submerged environments (Short *et al*., 2016). These systems are home to a wide range of ecological and economic activities (Royal Society, 2017), and provide numerous ecosystem services, including the provision of nursery habitats for commercially important marine species, raw materials, coastal protection, and enhancing water quality (Lau, 2013). Vegetated coastal systems are sometimes referred to as "blue carbon" ecosystems due to their role as carbon sinks (Mcleod *et al*., 2011; Pendleton *et al*., 2012). Thus, by capturing and sequestering carbon from the atmosphere, these blue carbon ecosystems play an important role in climate change mitigation (Fourqurean *et al*., 2012; Veettil *et al*. 2018; Lima *et al*. 2020; Ward, 2020).

Coastal ecosystems, when in pristine condition, naturally provide diverse benefits to both humans and nature. Therefore, effective nature conservation strategies are necessary to guarantee their continued or enhanced ecosystem service provision (Watson & Zakri, 2003; Rigo *et al*., 2021). The Millennium Ecosystem Assessment

(2005) uses a broad definition that equates 'the benefits people obtain from ecosystems' with the term 'ecosystem services.' As per the definition by the Millennium Ecosystem Assessment Board, 'an ecosystem is a dynamic complex of plant, animal, and microorganism communities and the non-living environment, interacting as a functional unit', including humans as an integral part of many ecosystems (Watson & Zakri, 2003). Amongst vegetated coastal systems, seagrass meadows have been identified as important ecosystem service providers, especially as there is strong evidence that healthy seagrass beds enhance the productivity of neighbouring systems like mangroves, salt marshes and coral reefs (de los Santos *et al*., 2020; Cziesielsk *et al*., 2021).

Seagrasses

Seagrass meadows have a pan-global distribution, being found in shallow coastal areas of all continents, except Antarctica (Garrard and Beaumont, 2014). Seagrasses occupy soft-bottom sediments of the world's oceans from the tropics to the temperate zones (World Resources Institute, 2005), extending from the intertidal zone to depths of up to 40 m (Gutiérrez *et al*. 2011). There is a high variation in the estimated global areal coverage of seagrass meadows, ranging from 17×10^6 to 60×10^6 ha worldwide (Hemminga & Duarte, 2000; Mcleod *et al*. 2011). This uncertainty highlights the need for more research, to better map and understand seagrass global distribution, including seasonal and long-term temporal variations (Garrard and Beaumont, 2014; Macreadie *et al*., 2018).

Seagrasses are marine angiosperms (**Figure 1**) adapted to exist fully submerged in brackish or salt water, where they promote sediment deposition, stabilise substrates, decrease water velocity and function as part of the estuarine filtration system, removing contaminants from the water column (Orth *et al*., 2006; Campagne *et al*., 2015). Seagrasses also provide a range of other ecosystem services to the marine environment, including nutrient cycling, supporting a range of commercially important fish species as a nursery habitat and as an important food source for mega-herbivores such as green turtles, dugongs, and manatees (Costanza *et al*., 1997; Hemminga & Duarte 2000; Orth *et al*., 2006; Björk *et al.,* 2008; Nordlund *et al*., 2018; de los Santos *et al*., 2020).

Seagrasses can also act as ecological engineers, altering their environment to improve conditions by reducing suspended sediment concentrations, which can increase light availability and reduce water column pollutant levels, resulting in improved conditions for seagrass growth and survival as well as other marine photosynthetic organisms (van der Heide *et al*., 2007 Paquier *et al*., 2014; Serrano *et al*., 2016). Seagrass canopies can also reduce wave attenuation, and this combined with a dense root matrix can further promote sediment deposition and prevent erosion (Potouroglou *et al*., 2017). Some species, particularly those with high canopy density and above ground biomass have been shown to reduce current velocities by up to 90%, resulting in net sediment accretion rates of up to 2 mm $year^{-1}$ (Hogarth, 2015).

Therefore, seagrasses directly and indirectly provide a range of ecosystem services, which vary by geographical region and genera (Cullen-Unsworth *et al*., 2014; Nordlund *et al*., 2016; Nordlund *et al*., 2018). The diversity of ecosystem services is categorised as provisioning (ecological goods, such as food, fisheries, etc. provided directly by seagrasses or indirectly by associated species), regulation and maintenance (ecological services, such as climate regulation, water filtration, and ecological processes), supporting (primary production, soil formation) and cultural (spiritual or knowledge values, such as recreation, tourism, and education) (Campagne *et al*., 2015; Nordlund *et al*., 2016).

Nature-Based Solutions

Nature-based solutions (NbS) are defined as innovations inspired and supported by nature, which provide environmental, social, and economic benefits, and help build resilience by benefiting biodiversity and supporting the delivery of a range of ecosystem services (Seddon, *et al*., 2019; Wild *et al*., 2020; UNEP, 2020). NbS can address such current and vital societal challenges as climate change and associated impacts, environmental pollution, food security and water scarcity. NbS include established approaches such as ecosystem-based adaptation, ecosystem-based disaster risk reduction, green and blue natural infrastructure, as well as the more recently described "natural climate solutions" (Cohen-Shacham *et al*., 2016, 2019; Griscom *et al*., 2017; Chausson *et al*., 2020).

The potential of seagrass ecosystems as NbS, including climate mitigation, is evidenced through the high carbon sequestration and storage potential, which could be used for CO_2 offsets in nationally determined contributions, particularly in the case of successful restoration (Stankovic *et al*., 2021; Lima *et al*., 2022). Stankovic et al. (2021) suggest that successful and well-designed restoration projects and conservation measures, could result in seagrass meadows contributing up to 1.43% towards CO_2 offset of countries' total emissions by 2030 (business-as-usual, BAU scenario). However, the climate solution potential of seagrasses is still one of the most poorly represented as a NbS (Chausson *et al*., 2020; UNEP, 2020; Veettil *et al*. 2021), partly because seagrass meadows are especially vulnerable to anthropogenic impacts from both adjacent terrestrial and marine systems (Unsworth *et al*., 2019). Such impacts can be physical, resulting in direct removal of plants, or chemical, polluting both the sediment and water (Mazarrasa *et al*., 2017). Moreover, storms and severe weather events, associated with climate change, can affect seagrass populations by uprooting plants and mobilizing sediments, increasing turbidity, and reducing water quality and light penetration (Cardoso *et al*., 2008). Additionally, fluctuations in sea temperature are considered the primary climate change related threat to seagrass ecosystems, which could lead to alterations in seagrass distribution and metabolism, subsequently reducing net autochthonous carbon sequestration potential (Clausen *et al*., 2014; Hyndes *et al*., 2016; Mazarrasa *et al*., 2018). Furthermore, sea level rise may alter habitat availability for intertidal seagrass species, and as projected by the IPCC (2019) with medium confidence under the RCP8.5 emission scenario by the end of the century, vegetated coastal ecosystems in general are at high risk of local losses.

Past studies estimate the value of coastal ecosystem services to be US$31.6 tr yr^{-1} covering seagrass meadows and algae beds as well as tidal marshes and mangroves (Bertram *et al*., 2021). However, compared to other coastal ecosystems (such as mangroves and corals) that also benefit humans, there has been substantially less research focus on identifying and valuing ecosystem services provided by seagrasses, mainly due to the absence of detailed information on marine habitat distribution and the difficulties in assessing both processes and functions (Maes *et al*., 2012; Himes-Cornell *et al*., 2018). Consequently, the value of seagrasses as an ecosystem is often not considered in marine management decisions, and rarely incorporated into NbS projects (Duarte *et al*., 2008; Grech *et al*., 2012; Chausson, *et al*., 2020). In addition, non-monetary values of seagrasses are important, with some studies assessing non-monetary values by using biological proxies, such as area coverage, the biomass of bird and mammal groups that seagrass supports, or the energy resources invested by nature when estimating the benefits of seagrass as a habitat (Plummer *et al*., 2013; Vassallo *et al*., 2013).

The lack of public awareness concerning the importance of the ecosystem services that seagrasses provide is arguably one the biggest threats to their conservation. This suggests that studies highlighting the importance of ecosystem service provision by seagrasses can raise the profile of this important habitat and provide support for their protection and conservation (Nordlund *et al*., 2018; Quevedo *et al*., 2020). Thus, this research evaluates and lists the services provided by seagrass ecosystems by conducting a comprehensive review of the literature, in order to identify potential gaps in knowledge and areas of focus or concern for the future. The aim of this review is to contribute to a better understanding of how seagrass ecosystem services have been studied so far, with the goal of constructing a knowledge-base for future NbS projects. The objective of this study is to review how the main ecosystem services provided by seagrass meadows have been reported over time to highlight the need for protection and preservation of their natural assets, in order to successfully develop NbS that incorporates these extremely productive ecosystems.

Methods

Literature Search

A systematic literature review was conducted in order to better understand the range of studies that have been published to assess the ecosystem services provided by seagrasses. The search centred on studies explicitly focused on ecosystem services (**Figure 2**). The literature search was conducted using the Web of Science scientific citation database. The studies were searched in the Web of Science Core collection (editions: Science Citation Index Expanded, Social Sciences Citation, Conference Proceedings Citation, Emerging Sources Citation, Conference Proceedings, Citation – Social Science & Humanities and Book Citation Science) considering the period between 1900 and March 2022, using the following search string applied to all fields: (seagrass*/ OR "sea grass*/") AND ("ecosystem/ service*/"), resulting in a total of 684 papers. A second search was conducted using the same search string but applied to the field topic (title (title, key words, and abstract), resulting in a total of 654 papers.

For the purpose of this study, the search focused on peer reviewed papers, excluding grey literature. It is likely that some of the literature on ecosystem services provided by seagrasses may have been published as working papers, government reports, or other additional grey literature sources. However, it is not feasible to develop search criteria that will identify all such possible studies within the topic of this study. Moreover, there are likely additional publications on studies for ecosystem services in seagrass habitats that do not mention the specific key words included in our search criteria.

Selection Criteria

In order to select articles to include in this review, all 684 publications were screened. Only publications that mentioned seagrass ecosystem services in the title, abstract or key words, or if the content was unclear reading the abstract, were retained, yielding 654 publications. Through this selection, the publications retained from the Science Citation Index Expanded were used for full-text reading and analysis. After full text reading, 105 publications (16% of all screened publications) were retained that focused on the description, valuation, or inclusion of one or more ecosystem services provided by seagrasses as the main topic of research, even if this was integrated into analyses with other coastal habitats such as, mangroves, salt marshes or coral reefs.

Data extraction

For those final selected publications, the publication year; type of publication; the ecosystems services discussed; the geographic area where the study was conducted; and the threats to the studied ecosystems were extracted. Ecosystem services were organised into categories based on the classification scheme defined by the Millennium Ecosystem Assessment (2005). The Millennium Ecosystem Assessment was chosen as a framework for this study as it was conducted as a multiscale assessment, with interlinked assessments undertaken at local, national, regional, and global scales, incorporating seagrass ecosystem services within their Marine, Coastal, and Island Systems section.

Results

Overall, there has been an ~~average~~ annual increase in the number of studies including evaluation of seagrass ecosystem services, ~~of 31.5%~~ over the 23~~19~~ years under study, with 19% (n=20) of the cumulative total of studies being published in 2021 (**Figure 3**). Studies ranged from reviews of existing ecosystem services, assessment of current threats, evaluation of public or stakeholders' perspectives, and knowledge gaps, to models for assessing ecosystem services and valuation.

Of the 105 studies analysed, 37% (n=39) had a global approach to seagrass ecosystem services, 34% (n=36) focused on specific global regions, mainly meadows in the Caribbean (n=5), Africa (n=5), and the Mediterranean (n=3), and 42 studies analysed seagrass ecosystem services at national level, representing 40% of the total number. The most prolific nations studied were the USA (n=9) and Spain (n=8), followed by Australia with 4 studies and Sweden and the UK, both with 3 studies each (**Table S1**). Approximately half of the analysed studies focused solely on ecosystem services provided by seagrasses (n=55), while the other half provided a combined approach, grouping seagrasses with other blue carbon ecosystems such as mangroves, coastal wetlands, kelp forests and coral reefs. Out of the 55 studies focussing on seagrass, 17 (16% of the total) concentrated on *Posidonia oceanica* (Linnaeus, 1813) meadows specifically. It was also noted that more recent studies focused exclusively on ecosystem services provided by seagrass habitats, whilst older ones usually combined seagrasses within wetlands and/or other coastal habitats such as oyster and coral reefs (**Table S1**).

Most studies described threats to seagrasses and their related ecosystem services. Although studies reported those threats differently, the nomination of threats provides an insight into the potential for changes in the area of intact seagrass ecosystems as well as challenges that resource managers likely face within each region, such as to fisheries. Within the studies evaluated, the greatest emphasis was placed on threats associated with land conversion, pollution, climate change, aquaculture, and unsustainable resource use (**Table S1**). The most cited threats in these studies have also been highlighted by the general literature on seagrass ecosystems, namely climate change, sea level rise, pollution, fishing, and urbanisation (Unsworth *et al*., 2019; Young *et al*., 2021; Moksnes *et al*., 2021).

Altogether, ecosystem services were reported 396 times within the selected studies, and these have been classified into types relating to provisioning, regulating, supporting and cultural services (**Table 1, Figure 4**). Although the wider literature regularly cites the large number of ecosystem services and benefits provided by seagrass systems, these are not always the central focus of research, rather being used as a means to justify the importance of studying these habitats. It has also been noted that a subset of ecosystem services tends to be researched much more frequently than others (**Figure 4**). For example, researchers tend to focus on carbon sequestration (n= 60), food provision (n= 49 studies), maintenance of habitat and biodiversity/nursery habitats (n= 37), storm protection/extreme events (n= 31) and opportunities for recreation and tourism (n= 29) far more than any of the other seagrass ecosystem services (**Table 1**). In addition, regulating services overall tend to be studied much more frequently than other categories of ecosystem services, representing 42% of the total with 166 mentions, whilst the least explored were provisioning services with 17% of total reports (n=66) (**Table 1; Figure 4**). Moreover, some seagrass ecosystem services identified by the Millennium Ecosystem Assessment are rarely, or sometimes never, assessed including, provisioning services of fuel or fresh water (**Table 1**).

In total, 17 studies provided valuation models for the ecosystem services described (**Table S1**). Services such as food security and raw material provisioning, and opportunities for recreation and tourism have mainly been assessed and used to value the ecosystem service provided by seagrass habitats. Researchers have used market prices to measure food, raw material, climate regulation (via carbon sequestration), and opportunities for recreation and tourism, while voided cost and replacement cost are generally used to value waste treatment and moderation of extreme events.

Discussion

Although the need to study ecosystem services for seagrasses is indicated by the increasing number of publications, findings are mostly focused on seagrass cover and distribution mapping (Hossain *et al*., 2014; Nordlund *et al*., 2016; Nordlund *et al*., 2018) except a few species-specific case studies focusing mainly on *Posidonia* spp. (Vassallo *et al.*, 2013; Campagne *et al*., 2015). Moreover, this review demonstrates that some ecosystem services are studied much more frequently than others (e.g., food provision in 47% of studies, carbon sequestration in 57% of studies), likely because of stakeholder interest and current climate change mitigation policies. Several important services are poorly addressed (i.e., medicinal, and genetic resources, air quality, regulation of water flow, biological control, spiritual experience) or entirely absent (i.e., fuel, ornamental resources, inspiration for culture/art) in the literature, most likely due to poor data availability and the difficulty of quantifying the extent of service provision. However, although this systematic review followed established search protocols, it limited the search to the wider term 'seagrass ecosystem services' within titles, key words or abstracts, which restricts the analyses of studies where seagrass ecosystem services do not feature in those sections, even though they might be indirectly evaluated or quantified in other sections. Consequently, for example, few studies from the UK were included in the search, although researchers such as Lima *et al*., (2020, 2022), Potouroglou *et al*., (2021), Green *et al*., (2018) and others have been assessing the UK's seagrass carbon stocks with the aim of promoting natural climate solutions. Another limitation to consider is that this review focused on scientific journal publications only, which discards regional and global reports on the assessment of seagrasses' ecosystem services and their potential as NbS, e.g. UNEP (2020). Nevertheless, this review suggests that there has been an increase in the inclusion of the term 'ecosystem services' in seagrass studies in more recent years, showing a positive trend of raising awareness of their importance as NbS.

Seagrass carbon stock analyses have been reported worldwide, even though there might be a bias of reported global estimates, which mainly focus on values from tropical and Mediterranean seagrass meadows dominated by larger species, like *Posidonia* spp. (Johannessen and Macdonald, 2016; Serrano et al., 2018; Lima et al., 2022). Although this demonstrates that many studies have been focusing on seagrasses' potential as NbS for climate change mitigation, these are not always evidenced as an ecosystem service provision, and even more rarely linked to the categories proposed by the Millennium Assessment, as described in this study. Therefore, despite a broad recognition of the importance of such data (Pascual *et al*., 2017), serious gaps in the identification of ecosystem services provided by seagrass ecosystems still exist, notably involving methodology, areal extent, and valuation of ecosystem services (Nordlund *et al*., 2018; de los Santos *et al*., 2020). The variability of ecosystem services across a seascape, including spatial (i.e. extent of a seagrass meadow and its ability to buffer storm waves) and temporal differences (seasonal fluctuations and density of seagrass biomass) may influence the assessment and quantification of some services and should be considered by researchers and policymakers (Barbier *et al*., 2011).

Mapping the services provided by seagrass ecosystems is key to evaluating temporal and spatial alterations to their provision, particularly when taking a regional approach, such as those reviewed in this study for the Caribbean and Mediterranean (de los Santos *et al*., 2020). Mapping ecosystem services is one of the requirements in ecosystem accounting, tracking alterations in natural assets and evaluating links with economic and human activities (Veettil *et al*., 2020). Despite advances in seagrass ecosystem service assessment studies and extent mapping, there are still large global and regional data gaps (Veettil *et al*., 2020; 2022), predominantly as a result of the in situ approaches that are typically used including scuba/snorkeling surveys (Gotceitas *et al*., 1997), ground-based sampling (Moore *et al*., 2000), and hovercraft-based mapping (McKenzie, 2003).

Even though projects focused on the protection and sustainable management of vegetated coastal environments, including seagrass, are not a novelty, such efforts are mainly aimed at generating benefits and services to local communities and biodiversity, as well as the fisheries and tourism sectors (Herr *et al.*, 2014; Mitsch and Mander, 2018). Unlike terrestrial ecosystems, few coastal programs have been established with the goal of conserving and restoring ecosystems as potential mechanisms for nature-based climate mitigation (carbon capture/ avoided emissions) solutions (Herr *et al.*, 2011; Gattuso *et al*., 2018). Chausson *et al*., (2020) assessed the six most represented ecosystem types when examining the effectiveness of nature-based interventions to address climate impacts and emphasised that only 13% of studies included coastal ecosystems, with only one study, out of 386, focused on seagrass ecosystems specifically. Herr and Landis (2016) highlight that even though 151 countries contain at least one blue carbon ecosystem (seagrass, mangrove, or saltmarsh) with 71 containing all three, only 28 countries include references to vegetated coastal systems in terms of climate crisis mitigation in their intended nationally determined contributions (INDCs). Hence, undertaking ecosystem service assessments, such as those presented in this review, could provide key data to identify conservation and management actions for these ecosystems to be incorporated in such strategies (Pabon-Zamora *et al*., 2008; Pascual *et al*., 2017).

Half of the studies in this review focused on seagrass meadows specifically while the other half incorporated neighbouring ecosystems in their ecosystem services appraisal. It has been reported that in order to comprehensively assess ecosystem services, it is necessary to incorporate the multiple and synergistic characteristics of ecosystems (Koch *et al*., 2009; Barbier, 2012). However, studies continue to focus on each service independently, even though ecological interactions suggest that there is connectivity between vegetated coastal ecosystems, which impacts the availability and/or quality of the services (Barbier *et al*., 2011). By assessing ecosystem services collectively, like some of the papers in this review, studies could better delineate between functions, services, and benefits to avoid the problem of double counting that may arise due to the fact that some services (i.e., supporting and regulating) provide the basis and inputs for the assessment of others (Boyd & Banzhaf, 2007; Fisher *et al*., 2009; Kumar, 2012). For example, in recent years, ecological niche modelling has been used as an alternative tool to predict the effects of climate change on seagrass ecosystem distributions (Valle *et al*., 2014; Davis *et al*., 2016; Chefaoui *et al*., 2018), the potential distributions of certain seagrass-associated species (March *et al*., 2013; Chefaoui *et al*., 2016; Jayathilake & Costello, 2018) and seagrass conservation priorities (Valle *et al*., 2013; Adams *et al*., 2016). Ecological modelling can be a useful and promising tool for seagrass restoration programs, as it is used to determine the most favourable environmental conditions for species growth by collecting large scale datasets for seagrass meadows, including variables such as: light intensity; seagrass coverage and biomass; sediment accretion rates; water velocity; sediment parameters and porewater nutrients (Valle *et al*., 2011; Adams *et al*., 2016; Stankovic *et al*., 2019; Horn *et al*., 2021).

To effectively include seagrass ecosystems in climate regulation policy, a comprehensive understanding of the factors that control carbon stocks, and sequestration rates, are urgently required (Lima *et al*., 2020). The reported loss of seagrasses capacity to sequester and store carbon is of high concern, highlighting the need for protection and conservation of these ecosystems (Unsworth *et al*., 2018). This should be undertaken to not only maintain the carbon stored in their sediments, but also to maintain important supporting ecosystem services linked to biodiversity, such as: critical feeding grounds for birds; important nursery areas for seabass; supporting threatened runs of migratory salmon and sea trout on their way to and from spawning grounds, as well as migration routes for eels to spawn at sea (Jackson *et al*., 2001; Hiscock *et al*., 2005; Lilley & Unsworth, 2014; Harding *et al*., 2016; Jones *et al*., 2018; Bertelli & Unsworth, 2018; de los Santos *et al*., 2020). To date, conservation programs are rarely based on the explicit consideration of threats and drivers for a specific seagrass meadow, and instead focus on conserving seagrass as part of a broader management plan incorporating other habitats or species, like many reviewed by this study (Jones *et al*., 2018). One way to improve this and highlight their importance would be to include conservation and protection of seagrass ecosystems in financing mechanisms involving the reduction of CO_2 emissions as a natural climate mitigation solution (Wylie *et al*., 2016; Herr *et al*., 2017; Howard *et al*., 2017; Barbier *et al*., 2018; Himes-Cornell *et al*., 2018).

Some seagrass areas have been reported to rival coral reefs in terms of supporting biodiversity, and when associated with adjacent mangrove and barrier reef systems, they can provide more protection services than the corals themselves and compensate for long term degradation of the reefs (Guannel *et al*., 2016). The indirect value of the supporting services provided by seagrasses, including providing shelter and nutrition to a range of marine species, adds to their wider ecological importance (Hogarth, 2015; Nordlund *et al*., 2016; Nordlund *et al*., 2018). However, many ecosystem services provided by seagrasses remain poorly studied, or not clearly referenced, especially indirect use values and non-use values (Himes- Cornell *et al*. 2018). With the recent focus on the climate mitigation potential of blue carbon ecosystems in the realm of international conservation (e.g., the Paris Agreement, UN SDG 14), coastal managers would benefit from a better understanding of the valuation of services provided by seagrass ecosystems. Jones and Unsworth (2016), further note that there are a wide range of risks associated with poor environmental management of seagrass meadows, particularly concerning the provisioning service of food security, the most frequent service described in this review, given their value as fisheries nursery habitats.

As a consequence of their sensitivity to disturbance and broad geographical range, seagrasses are considered to be excellent biological indicators to be included in intended nationally determined contributions (INDCs) as NbS (Pergent et al., 2015; UNEP, 2020). NbS are increasingly recognised as vital to achieving climate mitigation and conservation targets, with seagrass meadows in the UK and northern Europe, for example, being typically included in conservation law and agendas, either directly or indirectly (Harding *et al*., 2016; Jackson *et al*., 2016). However, studies suggest that these programs might not have been effective in protecting these ecosystems, with declines being consistently reported (Jones and Unsworth, 2016; Jones *et al*., 2018; Smale *et al*., 2019). Also, NbS, including seagrass restoration, are not typically among the lowest cost options and so do not form a major proportion of compliance markets, aimed to meet greenhouse gas emissions and climate change legislation (UNEP, 2020). Conversely, NbS are popularly represented in voluntary markets, with several methods being developed for seagrass restoration, including through the Verified Carbon Standard (Needelman *et al*., 2018; UNEP, 2020).

Conclusions

Following the publication of the Millennium Ecosystem Assessment (MEA, 2005) and the Economics of Ecosystems and Biodiversity report (Kumar, 2012), there has been increased interest in the development of national, regional, and global ecosystem services indicators. However, the full range of ecosystem services provided by seagrass ecosystems has not been appropriately quantified, suggesting that informed management decisions cannot be formulated. An increase in the geographic coverage of ecosystem services studies is recommended, especially in understudied areas such as Africa, South America and the Middle East, in order to improve value estimates by region and meadow type. Regional/global-scale datasets of spatially explicit seagrass species presence-absence, abundance, and estimates of their ecosystem service provision, although currently lacking, could support resource management, and facilitate global conservation targets demanded by multilateral environmental agreements, policies, and initiatives, especially those including natural climate solutions. Thus, future research needs to focus on: 1) incorporating less studied ecosystem services, especially those related to social relations and cultural heritage into valuation studies to fully grasp the natural capital provided by the seagrass ecosystem; 2) incorporating remote sensing techniques to better map seagrass meadows' areal extent and variability among species and sites, to better identify regions where losses of ecosystem services may be occurring; 3) use of ecological niche modelling as an ecosystem based management tool to better understand seagrass ecology and connectivity with other coastal habitats; 4) improved communication between regions and across disciplines, especially those that focus on ecosystem services provided by other coastal vegetated ecosystems adjacent to seagrass meadows, like salt marshes, mangroves, macroalgae and coral reefs. Results from this study showed a growing interest in researching ecosystem services provided by seagrass meadows, and also highlighted the threats hindering the provision of these services. Thus, more needs to be done, as detailed above, to make sure that the full scope of ecosystem services are recognised and appropriately assessed, to be effectively included in marine coastal management planning as NbS.

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Table 1: Integrated heat map representing the frequency of studies that developed seagrass ecosystem service valuation estimates for each ecosystem service category between 2000 and March 2022, per the Millennium Ecosystem Assessment Board classification scheme, (2005). Values of 0 represent no studies published for a particular ecosystem service that year.

		2000	2003	2004	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	Total
Provisioning Services	Food and fibre	1	0	1	0	1	0	0	1	3	0	2	6	4	3	2	4	3	5	9	4	49
	Fuel	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2
	Genetic resources	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	5
	Biochemicals / Fertilisers	0	0	1	0	0	0	0	0	0	0	0	2	0	1	0	0	1	0	3	1	9
	Ornamental resources	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	Fresh water	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Regulating Services	Air quality maintenance	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	2	0	7
	Carbon Sequestration	1	0	0	1	0	0	0	0	4	2	3	2	6	5	1	6	5	5	15	4	60
	Water regulation	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2	1	5
	Erosion control	1	1	0	0	1	0	1	0	1	0	0	2	4	3	1	0	1	1	5	1	23
	Water purification	0	0	0	0	0	0	0	0	1	0	0	1	3	2	1	2	1	3	6	2	22
	Waste treatment	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	3
	Disease regulation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
	Biological control	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	4
	Pollination	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Storm protection	0	0	0	0	1	1	0	0	2	0	1	0	3	5	1	4	2	4	6	1	31
	Climate regulation	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	6	0	9
Supporting Services	Soil formation	1	1	0	0	0	0	0	0	0	0	2	0	1	2	1	1	2	0	3	0	14
	Nutrient cycling	1	0	0	0	0	0	1	1	2	1	1	1	3	1	0	3	0	1	3	0	19
	Primary production	1	0	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	1	3	1	10
	Maintanance of biodiversity/Habitat	0	0	1	0	0	0	0	1	1	0	1	2	4	2	3	2	3	4	10	3	37
Cultural Services	Cultural diversity	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	5
	Spiritual and religious	0	0	0	0	0	0	0	0	0	0	1	2	1	1	0	1	1	0	1	0	8
	Knowledge systems	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	1	0	6
	Educational	1	0	0	0	0	0	0	0	0	0	1	1	2	1	0	0	2	0	4	0	12
	Inspiration	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	3
	Aesthetic	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	1	0	1	1	7
	Social relations	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2
	Sense of place	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2
	Cultural heritage	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	0	2	1	10
	Recreational and ecotourism	1	0	0	0	0	0	0	0	1	0	1	2	7	3	0	2	2	3	5	2	29

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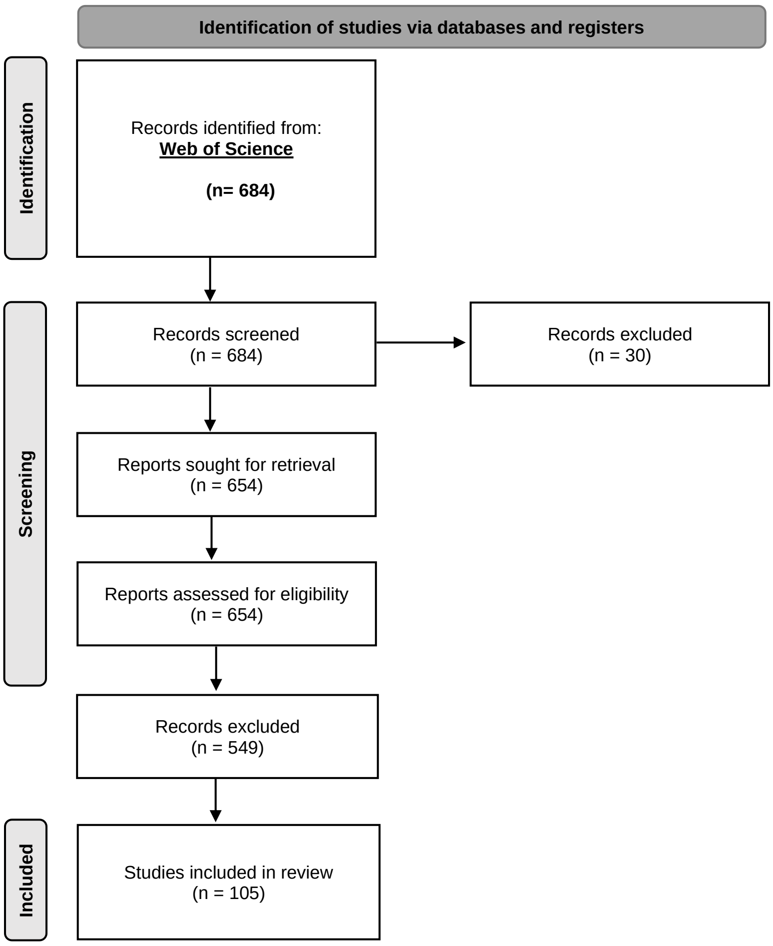
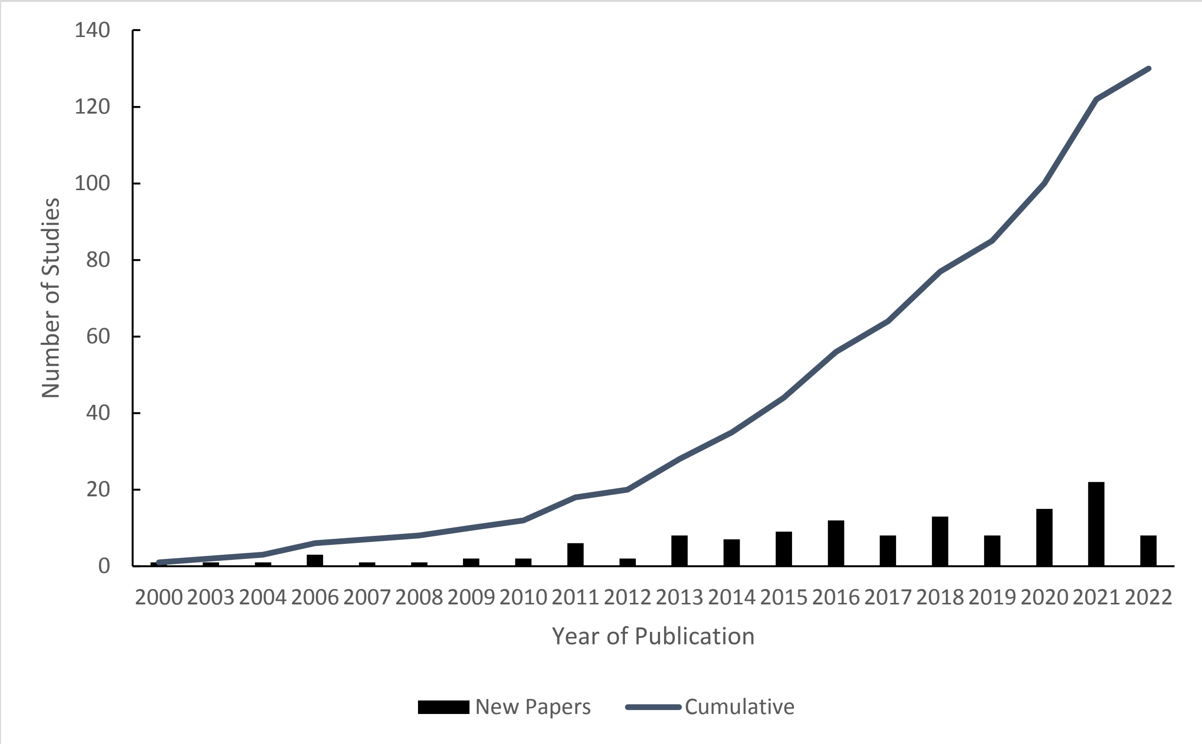
Figure 1: Seagrass meadow exposed during low tide. Patchy seagrass meadow dominated by Zostera angustifolia during low tide in Hayling Island, England, U.K. Photo credit: Mariana Lima, including anatomical scientific drawing of the seagrass Zostera marina (eelgrass), showing living above-ground (shoots and blades), below-ground (roots and rhizomes) components and seeds. (From: Watson, and Dallwitz, 1992).

Figure 2: Methodology and search criteria used in the systematic literature review following a modified version of the PRISMA (Preferred Reporting Items for Systematic Reviews) statement rules and template (Moher et al., 2010)

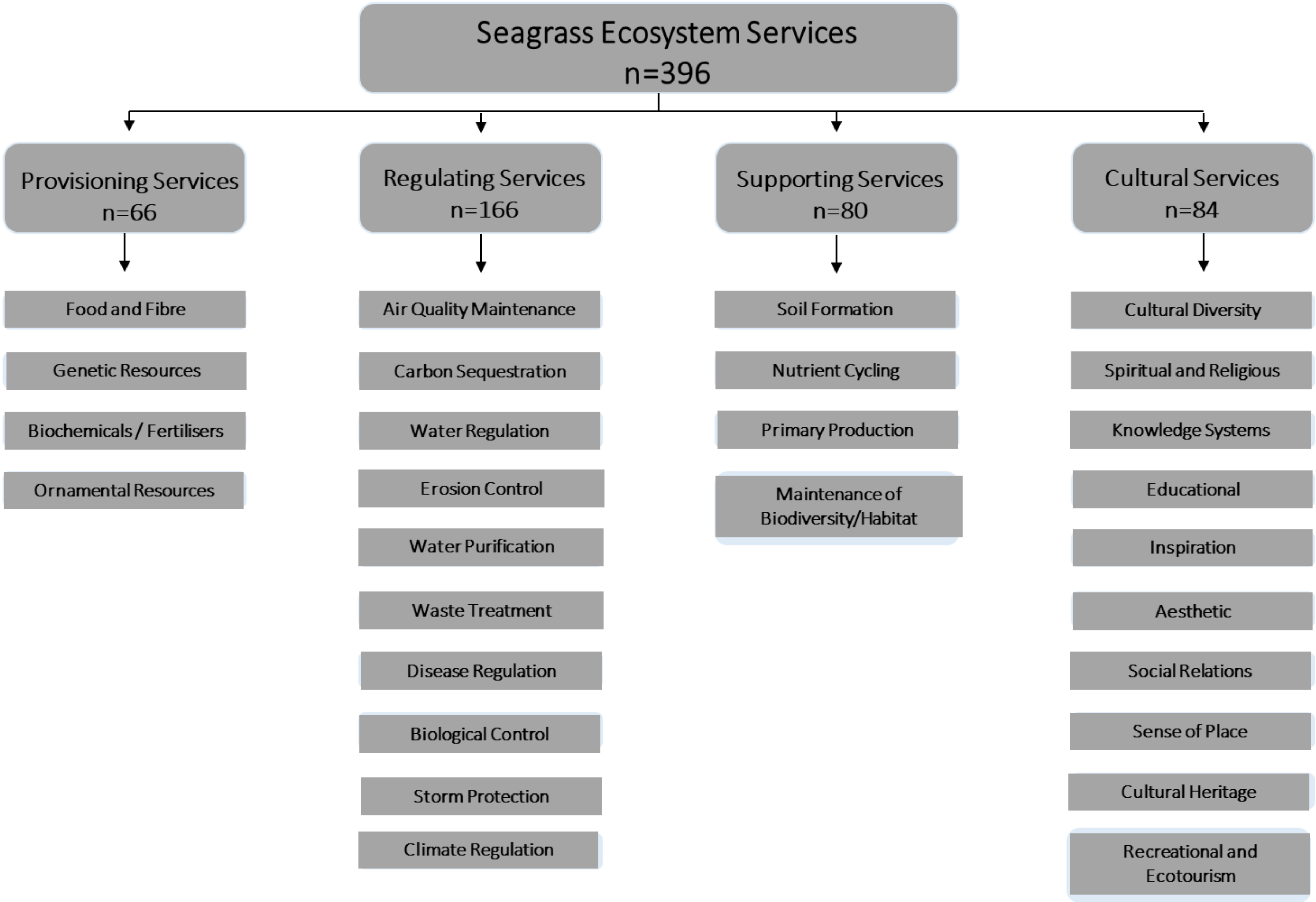
Figure 3: Number of Seagrass Ecosystem Service studies published per year from 2000 until March 2022, including cumulative line.

Figure 4: Schematic diagram showing all ecosystem services identified in this review, divided by the four main categories as suggested by the Millennium Ecosystem Assessment, 2005.


Identification of studies via databases and registers
Identification
Records identified from:
Web of Science
(n= 684)
Screening
Records screened
(n = 684)
Records excluded
(n = 30)
Reports sought for retrieval
(n = 654)
Reports assessed for eligibility
(n = 654)
Records excluded
(n = 549)
Included
Studies included in review
(n = 105)



Number of Studies
140
120
100
80
60
40
20
0
2000 2003 2004 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018 2019 2020 2021 2022
Year of Publication
New Papers
Cumulative


Seagrass Ecosystem Services
n=396
Provisioning Services
n=66
Regulating Services
n=166
Supporting Services
n=80
Cultural Services
n=84
Food and Fibre
Genetic Resources
Biochemicals / Fertilisers
Ornamental Resources
Air Quality Maintenance
Carbon Sequestration
Water Regulation
Erosion Control
Water Purification
Waste Treatment
Disease Regulation
Biological Control
Storm Protection
Climate Regulation
Soil Formation
Nutrient Cycling
Primary Production
Maintenance of Biodiversity/Habitat
Cultural Diversity
Spiritual and Religious
Knowledge Systems
Educational
Inspiration
Aesthetic
Social Relations
Sense of Place
Cultural Heritage
Recreational and Ecotourism

Mariana do Amaral Camara Lima
University of Salford
Room G37, Peel Building
Peel Building, M5 4WT
Manchester, UK.

01/04/2022

Dear Editorial Board,

We wish to submit a review article entitled "**A Review of seagrass ecosystem services: Providing nature-based solutions for a changing world"** for consideration by Hydrobiologia in the Special Issue – Ecosystem Services.

We confirm that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere.

This study provides a review of the main publications focused on ecosystem services provided by seagrass ecosystems, in order to identify any gaps in our knowledge of ecosystem service provision. Results showed that some ecosystem services, namely food provision, carbon sequestration and maintenance of biodiversity/nursey habitats receive a higher level of focus and attention than others, such as pollination, fuel, regulation of diseases and social relations, which are rarely, if ever, included in studies. It is clear that in order to fully comprehend the natural capital held by seagrass ecosystems, studies need to comprehend ecosystem services as a whole, and also combine and share results across global regions, to better understand the potential impacts of degradation and loss of these ecosystems worldwide. Suggestions also include applying novel technologies such as remote sensing and ecological niche modelling to address some of the main gaps in seagrass research, like meadows areal extent and connectivity within ecosystems, to better incorporate preservation of seagrass ecosystems in marine management plans. We therefore believe that this manuscript is highly appropriate for the special issue publication by Hydrobiologia because it consists of a comprehensive review on ecosystem services provided by an important marine environment - seagrasses.

We have no conflicts of interest to disclose.

Please address all correspondence concerning this manuscript to me at **M.doamaralcamaralima@salford.ac.uk**.

Thank you for your consideration of this manuscript.

Sincerely,

Mariana do Amaral Camara Lima

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