Impediments to Understanding Seagrasses' Response to Global Change

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ABSTRACT

Uncertainties from sampling biases present challenges to ecologists and evolutionary biologists in understanding species sensitivity to anthropogenic climate change. Here, we synthesize possible impediments that can constrain research to assess present and future seagrass response from climate change. First, our knowledge of seagrass occurrence information is prevalent with biases, gaps and uncertainties that can influence inferences on species response to global change. Second, research on seagrass diversity has been focused on species-level metrics that can be measured with data from the present - but rarely accounting for the shared phylogenetic relationships and evolutionary distinctiveness of species despite species evolved and diversified from shared ancestors. Third, compared to the mass production of species occurrence records, computational tools that can analyze these datasets in a reasonable amount of time are almost non-existent or do not scale well in terms of computer time and memory. These impediments mean that scientists must work with incomplete information and often unrepresentative data to predict how seagrass diversity might change in the future. We discuss these shortfalls and provide a framework for overcoming the impediments and diminishing the knowledge gaps they generate.

INTRODUCTION

Human activities, through fossil fuel emissions and widespread deforestation, have contributed to increased global temperature above pre-industrial levels (IPCC 2018). As a consequence, global increases in temperature and atmospheric carbon dioxide can influence species by altering their growth rates, physiological functions, sexual reproduction, distribution, community composition, and primary productivity (Campbell et al., 2006; Short & Neckles 1999). Such changes in environmental climate outside species' tolerable thresholds will cause some species to relocate in order to stay within their tolerance zones (Bradshaw & Holzapfel 2001; Parmesan, 2006; Miller-Rushing & Primack 2008; Anderson et al., 2012; MacLean et al., 2018). For instance, species on land generally ascend to higher elevations or latitudes as temperatures warm, but may run out of room, which can lead to local extirpation (Parmesan et al., 1999; Freeman et al., 2018). The sensitivity and responsivity of seagrasses or other marine species, whose distributional ranges lie at the land-sea margin and with very different evolutionary histories may show different responses to climate change.

Seagrasses are a major vascular plant clade of about 70 species belonging to the Alismatales, an order that includes ~4000 other non-marine species (Berry 2019). They are widely distributed across marine coastlines or estuarine environments, often growing submerged in marine water (Hemminga & Duarte 2000). Seagrasses display a wide variety of morphological diversity including turtlegrass (*Thalassia testudinum*) which forms long and jointed rhizomes, rhizome matts in *Posidonia*, ribbonlike leaves in eelgrass (*Zostera marina*), and paddle-shaped leaves in paddle grass (*Halophila decipiens*) (Figure 1). They play key ecosystem roles including primary productivity, nutrient cycling, and carbon sequestration (Hemminga & Duarte 2000; Duarte 2002; Les et al., 2002; Orth et al., 2006; McGlathery et al., 2007; Nordlund et al., 2018). Seagrass meadows are an important nursery ground for many invertebrates and fishes (Beck et al., 2001), and directly provide food for marine herbivores including manatees, dugongs, and green sea turtles (Green & Short 2003; Larkum et al., 2006). As threats from global climate change intensify, the impacts across seagrass communities are mixed. Some studies have found a decline in seagrass habitats especially in Australasia with decline rates of about 110 km^2 per year (Waycott et al., 2009). This pattern is not true in North America and Europe where seagrass communities are no longer in decline, but in fact show positive trajectories in some cases (de los Santos et al., 2019), perhaps as a result of the proliferation of seagrass monitoring and conservation programs such as Seagrass-Watch (https://www.seagrasswatch.org/) and SeagrassSpotter (https://seagrassspotter.org/). Indeed, the vulnerability to the impacts of climate change on seagrass communities may be scale or context dependent (Day et al., 2008).

A number of studies indicate that global climate change can impact seagrass communities in a variety of ways. Short & Neckles (1999) reviewed the potential effects of climate change on seagrass growth rates, reproduction and spatial distributions; Duarte et al. (2018) explored relationships between climate change and phenotypic variation in seagrasses (including physiological variation, propagation success, and herbivore resistance); whereas Erry et al. (2019) used a mesocosm experiment to assess response of a multi-trophic seagrass ecosystem to several global change factors. The findings overwhelmingly demonstrated that these factors in unison could lead to deleterious effects on seagrass ecosystems if they are unable to rapidly adapt to changes in climate. Similar trends have been observed for specific seagrass locations e.g., Great Barrier Reef (Waycott et al., 2007), Mediterranean (Pergent et al., 2014), tropical Pacific Ocean (Waycott et al., 2011), and Western Australia (Arias-Ortiz et al., 2018; Strydom et al., 2020); or in selected species (e.g., Chefaoui et al., 2018). Other threats to seagrass populations can be attributed to overexploitation, physical modification, nutrient and sediment pollution, and introduction and spread of invasive species (Zieman 1976; Ralph et al., 2006; Moksnes et al., 2008; Bryars et al., 2011; Dewsbury et al., 2016). By contrast, research to elucidate effects of global climate change on seagrass meadows and how to improve the prediction of future risks under varying scenarios of climate change have received less attention (Pernetta et al., 1994; Bijlsma et al., 1995; Short & Neckles 1999).

Here, we argue that the extension of research agenda to assess seagrasses' response to climate change may be constrained by at least three factors. First, our knowledge of seagrass occurrence information is widespread with biases, gaps and uncertainties that can influence downstream inferences. Second, most of the research on seagrass diversity has been focused on species-level metrics (e.g., species richness, endemism or threat) that can be measured with data from the present - but rarely accounting for the shared phylogenetic relationships and evolutionary distinctiveness of species. Species are not independent units but are lineages that evolve and diversify from shared ancestors (Diniz-Filho et al., 2013). Third, compared to the mass production of species occurrence records, computational tools that can analyze these datasets in a reasonable amount of time are almost non-existent or do not scale well in terms of computer time and memory. These impediments mean that scientists must work with incomplete information and often unrepresentative data to predict how seagrass diversity might change in the future. These shortfalls need be carefully recognized and remedied. The objectives of this review are therefore to first identify the knowledge gaps to understanding seagrasses' response to climate change, and secondly propose strategies and tools to overcome these impediments.

KNOWLEDGE GAPS IN SEAGRASS SAMPLING PRACTICES

Global change has become a central focus of modern ecology. Yet, our knowledge of how anthropogenic drivers affect seagrass evolutionary diversity is limited by a lack of biological data spanning the Anthropocene that equally represents all seagrass species. We define the Anthropocene as a period of profound human impact on biodiversity, characterized by widespread migration by humans as initiated by the Columbian Exchange circa 1492 (Nunn & Qian 2010). The vast amounts of specimens of seagrasses deposited in herbaria can serve as a historical lens into the ecological processes by which present-day seagrass diversity arose, are maintained, and may evolve in the future. However, occurrence records archived in herbaria and museums are non-randomly collected over space and time, and thus present biases and uncertainties that can complicate ecological inferences (e.g., Boakes et al., 2010; Meyer et al., 2016; Daru et al., 2018; Dias Tarli et al., 2018). As a consequence, the use of occurrence records has not fully permeated the field of global change biology. The gap between specimen availability and use is widening as hundreds of thousands of specimens are being mobilized through massive digitization efforts worldwide. We argue that sampling uncertainties in seagrass occurrence records can manifest in at least three ways: geographic, taxonomic, and temporal uncertainties (Figure 2). We distinguish between the uncertainties and describe how these limitations can inhibit progress in understanding seagrass response to global change.

Uncertainties in geographic sampling

Geographic bias is the disproportionate sampling of a species in some regions of its range relative to others (Meyer et al., 2016; Stropp et al., 2016; Daru et al., 2018; Menegotto & Rangel 2019). Seagrass geographic data is commonly available as point records or polygons. Point records are commonly derived from major data hubs such as the Global Biodiversity Information Facility (GBIF; Edwards, Lane, & Nielsen 2000), United Nations Environment World Conservation Monitoring Centre (UNEP-WCMC & Short 2020) or Ocean Biodiversity Information Facility (OBIS) whereas polygons are derived from the International Union for the Conservation of Nature's (IUCN) spatial database and United Nations Environment World Conservation Monitoring Centre (Green & Short 2003; UNEP-WCMC & Short 2020). Despite the fundamental importance of occurrence data for species distribution modeling, the sampling of seagrasses across most of their ranges are underrepresented in collections (Green & Short 2003). For instance, extensive spatial gaps exist across regions that harbor high concentrations of seagrass diversity, especially in Western and Central Indo-Pacific, whereas Europe and North America are well sampled (Figure 3) (see Methods and Source Data file in Supplementary Material for details). This pattern is consistent with previous studies. For example, Waycott et al. (2009) found wide sampling gaps in West Africa, northeast South America, and the northwest

Pacific area of the United States, most of which correspond to seagrass areas of endemism. Moreover, since biogeographic patterns are scale dependent, varying along spatial grains, geographic extents and taxonomic treatments (Jarzyna et al., 2018; Daru et al., 2020), the extent to which geographic uncertainties in seagrass sampling vary with spatial extent, grain size and taxonomic treatment remains poorly explored. However, it has been predicted that as grain size decreases, the knowledge gap in geographic sampling correspondingly increases (Hortal et al., 2015).

The mismatch between observed seagrass diversity and maps of survey efforts can be attributed to several factors: 1) knowing data exists in the first place and where it is, 2) harvesting data collected in native languages not common to science, 3) getting permission to access data collected under commercial license or from uncooperative governments, 4) validating data both spatially and taxonomically, 5) the difficulty in sampling specimens especially species in remote and inaccessible waters e.g., *Halophila decipiens* occurring >70 m deep in the Central Indo-Pacific (Short et al., 2007) or large parts of Northern Australia that are only accessible by helicopter, 6) lack of reliable research infrastructure e.g., West Papua and Papua New Guinea, 7) un-inhabited reef lagoons in large parts of the tropics and Western Pacific, 8) the cost of gathering long-term data (Wolfe et al., 1987), 9) perhaps a reversing trend of seagrass loss in Europe, North America, and subtropical Atlantic, e.g., increasing population trends in *Cymodocea nodosa* (Schäfer et al., 2021), *Zostera marina* and *Zostera noltei* (de los Santos et al., 2019; Guerrero-Meseguer et al., 2021), and 10) budget constraints for seagrass research. If seagrass species observations are made near accessible areas e.g., seaports, harbors or marine research stations, their application in analysis of species distribution modeling can compromise model performance (Kadmon et al., 2004; Lobo & Tognelli 2011; Bystriakova et al., 2012; Kramer-Schadt et al., 2013; Varela et al., 2014). In practice, this means that most observations only reflect the climate space of accessible areas, and correspondingly areas of human activities where surface temperatures are higher than in surrounding natural areas (Kalnay & Cai 2003). Additionally, regions known to contain seagrass meadows (e.g., Canada, Indonesia, and Russia) have inadequately mapped distributions, while other currently mapped regions most likely only represent a small portion of seagrass diversity (McKenzie et al., 2020). Targeting the places that are underrepresented in future collecting expeditions could remedy these limitations and aid in evaluating how species are responding to recent and future environmental change across biomes.

Uncertainties in temporal sampling

The sampling of seagrasses can manifest as temporal bias—the unbalanced collecting of specimens in some years or parts of a given year. This can influence conclusions drawn from analyses of such nonrandomly sampled collections records (Syfert et al., 2013). Temporal data is increasingly used in a wide range of applications in ecology and evolutionary studies including tracking changes in phenology – the timing of seasonal events such as flowering, leafing and fruiting – and monitoring the spread of invasive species (Iler et al., 2013; Veeneklaas et al., 2013; Meerdink et al., 2019). Yet, while there is general agreement that climate change can influence phenological patterns by disrupting the timing of life cycle events and consequently drive changes in fitness and population demography (Ovaskainen et al., 2013; CaraDonna et al., 2014; Thackeray et al., 2016; Kharouba & Wolkovich 2020), most have been observed in terrestrial species and to a lesser extent in marine flowering plants. In a meta-analysis of GBIF occurrence records over the course of 250 years (1770-2020) to understand the nature and evolution of seagrass sampling, sparser records were observed in earlier years and high collection densities between the 1900s and present-day (Figure 4). Although over the 250-year time span, occurrence data was absent for a total of 131 years. Seasonally, seagrass specimens were overwhelmingly biased toward spring and summer months (regardless of hemisphere location) for most marine ecoregions including Temperate Southern Africa, Temperate Australasia, Temperate Northern Pacific, and Temperate Northern Atlantic (Figure 5; see Methods and Source Data file in Supplementary Material). Interestingly, these periods are spanned by comprehensive time series data of ocean climate including sea temperature and salinity (Benway et al., 2019). This means that the time series of changes in seagrass communities across years or seasons are fewer than the available climate records (cf. Duarte et al., 1992). As a consequence, the nonrandom sampling of seagrasses in some years or parts of a year could mean that occurrence records are not reliable sources of phenological change driven by climate or population demography. If seagrasses are collected only when it is climatically convenient coupled with lack of reproductive structures on most specimens (Pearson et al., 2020), botanists may miss important phenological events such as winter bud formation, which protects the embryonic shoot of species during development and elongation (van der Schoot et al., 2013). Similarly, climate change can influence population demography through range change (Hunter et al., 2010; Dalgleish et al., 2011; Hugo 2011; Gaillard et al., 2013; Selwood et al., 2015) or facilitate the spread of invasive species (Hellmann et al., 2008; Clements & Ditommaso 2011; Vicente et al., 2013; Hou et al., 2014; Thapa et al., 2018). However, the skewed sampling of seagrass occurrence data suggests that the data is insufficient to track demographic changes or monitor spread of invasive species. We recognize that several aspects can influence seagrass sampling across years or seasons. For instance, some seagrass species are annuals, completing their life cycle within one growing season (e.g., *Halophila decipiens*). Other reasons include inaccessibility to most sites in the West Indo-Pacific during monsoon times, resulting in overrepresentation of specimens during maximum growing season/flowering season.

Uncertainties in taxonomic sampling

The sampling and collection of seagrass data may be disproportionately higher in some taxa over others (Hortal et al., 2008). Taxonomic uncertainty can manifest as phylogenetic bias and be assessed by testing for phylogenetic signal in collection frequency. A strong phylogenetic signal – closely related species share similar collecting frequency – would suggest phylogenetic bias in collections (Daru et al., 2018). Phylogenetic bias can hamper prospects of identifying species that are climate change indicators and those most likely to be affected by future climate change, especially given that species' response to climate change tends to be phylogenetically nonrandom (Willis et al., 2008; Davis et al., 2010; Davies et al., 2013). A phylogenetic analysis of long-term monitoring data in Concord Massachusetts, for instance, revealed a strong association between change in abundance with flowering time response such that the response traits are shared among closely related plant species (Willis et al., 2008). However, taxonomically nonrandom collection may mask such patterns and therefore bias conclusions of seagrass response to climate change. These data limitations may result from a research focus on specific seagrasses lineages over other groups or simply lack of data on some species. For example, Coyer et al. (2013) estimated divergence times in 20 species in the family Zosteraceae at 14.4 Ma, whereas Dilipan et al. (2018) assessed phylogenetic relationships by focusing on only family Hydrocharitaceae. Not only do these clade-based approaches point to different divergence times, but the phylogenetic reconstructions also used different gene regions with likely different rates of evolution. Seagrass occurrence data on GBIF tends to display a weak phylogenetic signal in the tendency of closely related species to be sampled similarly; with an average of ~9 specimens per species representing most *Halophila*, and ~6-9 specimens per species representing most *Zostera*, whereas *Halodule* and *Posidonia* had far fewer records (Figure 6; see Methods and Source Data file in Supplementary Material for details).

Another factor that can induce taxonomic bias is the lack of comprehensive phylogeny for seagrass species. Inferring evolutionary patterns based only on phylogeny of the taxa within the community of interest without fully accounting for the overall phylogenetic diversity of the entire lineage can potentially lead to spurious results (Park et al., 2018). The available DNA sequences of seagrasses in GenBank/EBI are sufficient to construct a molecular phylogenetic tree for only 55 (of 72) species (Daru & le Roux 2016). The 17 species without available DNA sequences are often manually grafted to the molecular tree in a multichotomy to the node of their close relatives using a Bayesian framework (Thomas et al., 2013). Such incomplete sampling or misplaced taxa on the phylogeny can influence the final tree topology and compromise rates of evolution (Nee et al., 1994, FitzJohn et al., 2009), especially when biases are also geographically nonrandom (Daru et al., 2018). Even with complete DNA sequences for all seagrass species, there are large uncertainties in the estimation of divergence times, and unknown evolutionary models linking phylogenies to underlying ecological traits and life history variation (Diniz-Filho et al., 2013). Moreover, the polyphyletic nature of seagrasses, drawing from several lineages within the Alismatales, might also compound our understanding of phylogenetic sampling biases.

The aforementioned sampling uncertainties can combine with each other in several ways. Taxonomic uncertainty can influence all other uncertainties because it reflects knowledge gaps on the fundamental unit of ecology and evolutionary biology. Geographic uncertainty is strongly influenced by temporal uncertainty as limited accumulation of data over time can alter accurate estimations of species' range size or population demographic history (Pybus et al., 2000, Drummond et al., 2005). Similarly, geographic uncertainty can compromise estimates of species' phenological response to climate change or demographic change, owing to lack of geographical coverage in many regions (Poelen et al., 2014). Ultimately, these sampling uncertainties are human artefacts such that any personal preferences, biases, and proclivities of collectors can greatly skew our understanding of seagrass diversity.

GAPS IN KNOWLEDGE OF SEAGRASS EVOLUTIONARY DIVERSITY

Understanding what drives variation in the distribution of biodiversity can provide insights into the ecological and historical processes underlying community assembly (Cavender-Bares et al., 2009) and for prioritizing conservation (Kreft & Jetz 2010; Holt et al., 2013; Daru & le Roux 2016). However, data gaps in the sampling of seagrasses (as outlined above) can influence estimates of broad-scale patterns and underlying processes (e.g., extinction, speciation and niche conservatism). Traditionally, identifying broad-scale patterns in seagrasses has been based on species-level metrics (e.g., species richness, and endemism) (Short et al., 2007; Mtwana et al., 2016; Duffy et al*.,* 2019). Although indispensable in providing baseline biodiversity knowledge, these metrics alone fail to detect the substantial evolutionary and conservation implications captured by the shared phylogenetic relationships and evolutionary distinctiveness of species (Mace et al., 2003; Redding & Mooers 2006; Cadotte 2013). Recent approaches harmonized metrics that consider evolutionary components, for example, phylogenetic diversity (Faith 1992), evolutionary distinctiveness (Redding & Mooers 2006), phylogenetic endemism (Rosauer et al., 2009), or a combination of these metrics. As pressures from climate change induced by anthropogenic activity mount, we will eventually observe range shifts and losses that can erase unique evolutionary history (Waycott et al., 2009). There is some evidence that evolutionarily distinct temperate seagrass assemblages might be disproportionately at risk of extinction (Daru et al., 2017), which could elevate losses of phylogenetic diversity (Redding et al., 2008). However, the associated directionality of species' responses to climate change and impact on phylogenetic diversity under a scenario of nonrandom extinction is unclear (Purvis et al., 2000). This means that as global temperatures increase, tropical seagrass species might be capable of expanding their distributions (Beca-Carretero et al., 2020) into regions traditionally utilized only by temperate seagrass species. This can induce selection pressures on temperate species that can result in the loss of distinct evolutionary diversity of seagrasses as the available climate space for temperate species is reduced by warming temperatures. Such pressures would inhibit our ability to understand the evolutionary history of seagrasses, as evolutionarily distinct species are lost or greatly reduced.

The global decline of seagrasses along a latitudinal gradient is imbalanced, with greater declines documented in temperate than tropical regions, requiring urgent conservation action (Hauxwell et al., 2001; Orth et al., 2006; Moksnes et al., 2008; Bryars et al., 2011; Erry et al., 2019). The recent finding that temperate seagrass assemblages tend to be those that are most evolutionarily unique also warrants concern given that their extinction would result in a greater loss of phylogenetic diversity (Daru et al*.,* 2017). In this regard, the familial membership of threatened seagrass species across marine ecoregions (see Methods and Source Data file in Supplementary Material) showed a tendency of threatened species in the Temperate Northern Pacific and Tropical Eastern Pacific clustering within similar families (Figure 7). This phylogenetic and taxonomic structuring suggests that evolutionary history is an important predictor of species decline, possibly reflecting a non-random pattern of extinction risk (Purvis et al*.,* 2000). Van Allen et al. (2012) demonstrated the importance of life-history traits for predicting how natural assemblages are likely to be impacted by anthropogenic and climatic disturbances using modeled declines in population growth rates under simulated stochastic disturbance. With regard to species extinctions and extinction risk, an important link has been identified between the loss of species and the loss of unique evolutionary history (NRC-US, 2008). Furthermore, the extinction of evolutionarily distinct or paleoendemic species can elevate losses of evolutionary history (Veron et al., 2015). These patterns might be indicative that seagrasses are characterized by species that subtends longer phylogenetic branches perhaps representing once diverse clades that have been lost through historical extinctions.

As seagrasses are increasingly threatened along their taxonomic structure spanning several marine ecoregions, we argue that seagrass extinctions are unlikely to be random. Previously, Short et al. (2011) determined that roughly 14% of seagrass species were at an elevated risk of extinction based on the IUCN's Red List of Threatened Species criteria. Currently, the IUCN indicates that 31% (22 out of 72) of seagrass species are in global decline, and 22% lack information for proper assessment of conservation status (IUCN, 2020). Therefore, the question of why some species persist while others decline across regions will require an understanding of the shared evolutionary history underlying changes in species richness and composition

(Waycott 1999; Arnaud-Haond et al., 2010; Massa et al., 2013). With many species' ranges greatly reduced or unknown, it is even more challenging to track patterns in seagrass population successes or failures that could be indicative of their resilience to climate change. In the absence of these key insights for the adaptive potential of seagrass species, we are unable to fully predict how individual species of seagrasses will respond to drastic, widespread environmental changes.

In order to facilitate effective conservation action, it is important to accurately determine which species are currently at the greatest risk for extinction, and which species will be at risk in the future. One successful approach has been to collect expert opinion data to prioritize seagrass management actions at regional scales (Grech et al., 2012) for species that may be unequally impacted. To this end, phylogenetic information can be very useful for predicting vulnerabilities at individual or familial levels (Gallagher et al., 2015). For example, families with a high proportion of species in global decline include Zosteraceae, Hydrocharitaceae, Posidoniaceae, and Cymodoceaceae; with Zosteraceae contributing about half of the total number of species in decline (Figure 8). Therefore, Zosteraceae and other evolutionarily similar families may possess a phylogenetic signal for extinction pressures. Families with seagrasses having unknown population trends include Hydrocharitaceae, Cymodoceaceae, Ruppiaceae, Posidoniaceae, and Zosteraceae according to the IUCN (see Methods and Source Data file in Supplementary Material for details). These groups are of high conservation concern given that species associated with these families may be currently threatened or already in decline without notice. Such population trends, or lack thereof, imply that certain species of seagrasses may be too heavily impacted in the future to prevent complete losses or extinctions given the rapid pace of climatic change.

SHORTFALLS IN COMPUTATIONAL TOOLS FOR ASSESSING SPECIES RESPONSE TO CLIMATE CHANGE

It is possible that the aforementioned impediments can be solved by increasing biological knowledge and computational capacity. However, compared to the mass production of occurrence records and climate data, tools that can analyze these datasets in a reasonable amount of time are almost non-existent or do not scale well in terms of computer time, memory, or other resources. This is particularly true for seagrasses that have wide geographic ranges, colonizing every coastline. As a consequence, ecologists and conservationists wishing to address questions related to seagrass response to climate change may be deterred by lack of analytical tools.

The occurrence data typically used for species distribution modeling is generated from massive digitization of museum records and citizen science campaigns (e.g., Seagrass-Watch, https://www.seagrasswatch.org/) and are often available as point records; whereas global oceanographic variables are measured by instruments on satellites daily (NOAA Climate.gov, 2020), which increase the size of the dataset many-folds. This exponential increase in species occurrences and oceanographic information inflate the size of running time for modeling algorithms (Farley et al., 2018; Allen et al., 2019), and consequently increases the challenges for visualizing downstream patterns. In Figure 9, the number of seagrass occurrence records in GBIF has increased over time. Where there used to be access to only a few dozen records, the rapid expansion of biodiversity occurrence data has now made it common for there to be a few thousand records per species (see Source Data file in Supplementary Material). This poses computational challenges for researchers. For analysis of species distribution modeling under different representative concentration pathway scenarios, for instance, researchers rapidly run into a spatial scale exponentiation problem. At a spatial resolution of 0.5 degrees (equivalent to ~50 km at the equator) covering the geographic ranges of seagrasses, there are 201,600 possible pixels for the algorithm to evaluate from. Computing probabilities across a 201,600-possibility data frame is a challenge. Such large-scale analysis can easily reach thousands of bytes and analysis using current tools would be prohibitively expensive computationally.

Presently, the software that can facilitate analysis of species distribution modeling of seagrasses includes *maxent* (Steven et al., 2017), *dismo* (Hijmans et al., 2011), *biomod2* (Thuiller et al., 2014), *esdm* (Woodman et al., 2019), ModEco (Guo & Liu 2010), SDMtoolbox 2.0 (Brown et al., 2017), ArcGIS and ARCMap. Several of these packages contain some statistical capabilities by integrating occurrence information and climate data. For instance, *biomod2* facilitates species distribution modeling by averaging across different methods including generalized additive models, generalized linear models, generalized boosting trees, maximum entropy, and random forest (Thuiller et al., 2014). However, these packages differ in their inferences, and analytical and computational capacity to process the massively mobilized occurrence records spanning tens of thousands of pixels across the globe (depending on the measurement scale). Some of these packages are developed for use in command-line while others are graphical user-interface (GUI). Most packages are developed to address a specific biological question and may have restricted analytical options that can limit computational flexibility. Ultimately, scientists wishing to address more complex hypotheses will have to use a compilation of multiple computational workflows.

More recent approaches to scale existing software to handle the exponential growth of biodiversity datasets include developing parallel algorithms (McCallum 2011) and using modern computational architectures, such as multicore systems, graphics processing units, and supercomputers (Maruyama et al., 2011). The advantages of these methods are that they provide reproducible source codes. However, they might require the user to have a good background in high performance computing. These limitations should not detract from exploring other outstanding questions that remained to be addressed with the available tools: 1) What are the effects of reduced area and increased isolation of marine habitats? 2) Where will seagrass species disperse to under alternative scenarios of climate change? and 3) How have anthropogenic activities e.g., marine pollution, sedimentation, and coastal urbanization changed the geography of seagrasses?

OVERCOMING THE IMPEDIMENTS

Seagrass occurrence records are increasingly being utilized in biogeographical investigations and prioritizing conservation (Valle et al., 2014; Chefaoui et al., 2018; Jayathilake & Costello 2018; Beca-Carretero et al., 2020; Heck et al., 2020). As possible solutions for the geographic uncertainty, we suggest enhanced funding for local, regional, and global inventories such as SeagrassNet for seagrass habitats in the Western Pacific (Short et al., 2006), Seagrass-Watch in Australasia (McKenzie et al., 2000, 2009), ResilienSEA (http://resiliensea.org/) in West Africa, Texas Seagrass Monitoring program (http://www.texasseagrass.org/), SeagrassSpotter (https://seagrassspotter.org/) a global tool for locating seagrasses, or Zostera Experimental Network (http://zenscience.org) for eelgrass (*Zostera marina*). Overcoming gaps in geographic sampling can also include collectors using best practices for collecting and vouchering specimens such as capturing accurate geolocations. It could also require the digitization and mobilization of vouchered seagrass specimens stored in herbaria and museums across the world. The iNaturalist project is a platform for sharing species observations along with geographic coordinates for terrestrial organisms and can be leveraged for filling in the data gaps in seagrass sampling. Kew's Plants of the World Online portal (POWO) provides distribution information on the seed-bearing plants of the world based on level 3 of the Taxonomic Diversity Working Group distribution scheme which corresponds to country borders (POWO 2019) and can be extended to cover seagrasses as well. High resolution cameras attached to unmanned aerial vehicles can be deployed to survey seagrasses in remote and inaccessible waters; however, special permits can often be required to access some sites (Johnston 2019).

Species distribution models – the statistical estimation of species geographic distributions based on only some known occurrences and environmental conditions (Peterson et al., 2011) – can also provide an unbiased and easily interpretable estimate of improving representativeness and coverage of seagrass distributions. For example, a recent species distribution model predicts more than two-fold increase in the potential global distribution of seagrasses (Jayathilake & Costello 2018). However, the accuracy of this prediction has attracted particular scrutiny because of inconsistent measures and widespread sampling gaps in seagrass occurrence records (McKenzie et al., 2020). Additionally, modeling approaches can contribute other useful measurements of seagrass meadows such as assessing ecosystem services as well as estimating broad-scale seagrass resources as was exemplified by Collier et al. (2021) who used historical data to accurately predict the below-ground biomass of five seagrass species. Because geographic scale is an important consideration in ecological analyses (Jarzyna & Jetz 2018; Daru et al. 2020), a multi-scale approach varying along spatial extents (local, regional and global) and grain resolutions should be considered in assessing seagrass response to global change and model testing. Temporal uncertainty can be diminished by carrying out new field surveys that are more consistent and evenly distributed across seasons and years. Collectors should use best practices such as capturing and documenting accurate dates of collection. For the taxonomic uncertainty: increased support for marine plant taxonomy and advances in taxonomic publications could minimize biases. Next-generation DNA sequencing combined with bioinformatics (Taberlet et al., 2012) will help diminish taxonomic uncertainty such as sequencing old herbarium specimens of very rare species such as *Halodule bermudensis*. The rapid growth of large databases such as GenBank (http://www.ncbi.nlm.nih.gov/genbank), SeagrassDB (Sablok et al., 2018), and Treebase (http://www.treebase.org), allows researchers to download available phylogenies or DNA sequences to build their own (Morell 1996; Piel et al., 2000; Page et al., 2007). Taxonomic bias can also be reduced by targeting future collecting in poorly sampled clades.

Improvement of analytical and computational tools is an important priority for handling the analyses for large-scale comparative analyses of seagrass species. For instance, the US National Science Foundation-funded software *BiotaPhy* facilitates integration, data collection and analysis by connecting to existing data repositories such as the Open Tree of Life, iDigBio, and Lifemapper (BiotaPhy 2020), whereas the open-source package *sampbias* allows quantification of geographic sampling biases in species distribution data (Zizka et al., 2020). The R software package *phyloregion* – designed for biogeographic regionalization and macroecology – can overcome some computational challenges (Daru et al., 2020). It contains tools for biogeographical regionalization, macroecology, conservation, and visualizing biodiversity patterns, and has potential application in diverse fields including evolution, microbial diversity, systematics, ecology, phylogenetics, and many others (Daru et al., 2020). We expect that the proliferation of more open-source analytical tools to greatly facilitate comprehensive understanding of seagrass sensitivity to ecological change driven by anthropogenic causes.

CONCLUDING REMARKS

Here, we outlined impediments that limit progress in understanding seagrass sensitivity to global change induced by human activities. These knowledge gaps are interconnected and represent only few of the possible issues related to research in seagrass diversity and evolution. Taxonomic uncertainty can influence all other types of uncertainties as it reflects knowledge gaps on the fundamental unit of ecology and evolutionary biology. The geographic and temporal uncertainties are strongly related and capture knowledge gaps about species distributions in space and time, respectively. Even when the aforementioned impediments are resolved, many of the critical questions about seagrass sensitivity to global change, can be out of reach for scientists without the right analytical tools. The recent development of efficient and replicable computational tools, massive mobilization of natural history collections, and increased funding for seagrass research could remedy these shortcomings. Most of the management tools designed for use in developed countries can be extended to remote areas in developing countries where most seagrass diversity resides e.g., the Central Indo-Pacific. Although research on a single taxon or selected taxa is useful to a certain extent, species are lineages that evolve and diversify from shared ancestors, suggesting an integrative approach that accounts for their shared phylogenetic relationships.

AUTHOR CONTRIBUTIONS

BHD conceived and designed the study. BMR ran the analyses with help from BHD. BMR wrote the paper with substantial contributions from BHD. Both authors approved the submitted version.

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SUPPLEMENTARY MATERIAL

Supplementary Methods can be found in the online version of this article.

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FIGURE LEGENDS:

Fig. 1 Morphological diversity of selected species of seagrasses. (A) *Thalassia testudinum* (turtle grass) bed with view of jointed rhizomes, San Salvador Island, Bahamas. (B) *Posidonia oceanica* (Neptune grass) meadow with view of rhizome matts, Portofino, Italy. (C) *Zostera marina* (eelgrass) with ribbon-like blades. (D) *Halophila decipiens* (paddle grass) with paddle-shaped blades. (https://commons.wikimedia.org and https://calphotos.berkeley.edu/).

Fig. 2 Interactions between sampling uncertainties indicating the extent of influence of each uncertainty on the others. Taxonomic uncertainty affects all other uncertainties whereas arrows indicate direction of influence between the other two. However, all three types of uncertainty ultimately reflect the personal preferences, biases, and proclivities of collectors.

Fig. 3 Gaps in geographic sampling of seagrasses. (A) Seagrass occurrence records showed strong density of sampling in temperate regions, while sampling within the tropics was generally low. (B) Geographic distribution of seagrass known species richness based on expert delineated polygons. Source data are provided as a Source Data file.

Fig. 4 Temporal sampling of seagrasses reveal drastic increases midway throughout the 18th century. Temporal data from seagrass records over the course of three centuries (roughly 1700-2000) display dense amount of sampling records accumulating after 1850. Each dot represents an occurrence record of a seagrass in Julian day of year format, with the color gradient representing recent years with colder color tones, and older years represented by warmer color tones. These data also support the previously identified global trend of increased sampling occurring predominantly within the summer months (early June through early October). Source data are provided as a Source Data file.

Fig. 5 Temporal trends in seagrass sampling are not consistent across seasons within marine ecoregions of the world (MEOWs). Temporal data from seagrass occurrence records were converted into Julian day of year format in order to analyze trends in the monthly sampling of seagrasses for all MEOWs. The blue line around each temporal sampling plot represents seagrass sampling density in monthly intervals over an extensive time period (1770-2019), with corresponding temporal sampling plot for each MEOW. Seagrass sampling rates increase during summer seasons associated with northern and southern hemispheres. The central plot provides a reference for the geographic location of each MEOW included in the analysis. Source data are provided as a Source Data file.

Fig. 6 Phylogenetic bias in seagrass sampling. Phylogenetic distribution of the number of specimens sampled per seagrass species to assess the tendency of closely related species to be similarly collected. No statistically significant phylogenetic signals were detected, although there was slight favoring for sampling of the *Thalassia, Enhalus,* and *Halophila* genera over other seagrass genera. Source data are provided as a Source Data file.

Fig. 7 Correlations of family ranks possessing threatened seagrass species across marine ecoregions of the world (MEOWs). The pairwise correlational analysis assigned values based on the level of overlap of seagrass families across MEOWs that possessed seagrass species classified as threatened by the International Union for Conservation of Nature. Low correlation values were generally reported between temperate and tropical MEOWs, indicating that the threatened seagrass species in these regions are unique to those areas. Source data are provided as a Source Data file.

Fig. 8 Taxonomic distribution of extinction risk in seagrass. Population status of seagrasses were assessed using the classifications set forth by the International Union for Conservation of Nature. Proportion of threatened species was assessed as number of threatened species in a family divided by the total number of species assessed within that family. When comparing the proportions of threatened species per family to the calculated 95% confidence interval, 3 families were significant: Zosteraceae, Posidoniaceae, and Hydrocharitaceae. Source data are provided as a Source Data file.

Fig. 9 Temporal change in the amount of seagrass occurrence records over time. Seagrass point records downloaded from GBIF were mapped over time based on the chronological date listed in the occurrence data for each record to demonstrate that seagrass occurrences have greatly increased within recent decades. This indicates that analyses with these data will be computationally expensive. Source data are provided as a Source Data file.