

Article

Linking Coral Reef Remote Sensing and Field Ecology: It's a Matter of Scale

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Abstract: Remote sensing shows potential for assessing biodiversity of coral reefs. Important steps in achieving this objective are better understanding the spectral variability of various reef components and correlating these spectral characteristics with field-based ecological assessments. Here we analyze >9400 coral reef field spectra from southwestern Puerto Rico to evaluate how spectral variability and, more specifically, spectral similarity between species influences estimates of biodiversity. Traditional field methods for estimating reef biodiversity using photoquadrats are also included to add ecological context to the spectral analysis. Results show that while many species can be distinguished using *in situ* field spectra, the addition of the overlying water column significantly reduces the ability to differentiate species, and even groups of species. This indicates that the ability to evaluate biodiversity with remote sensing decreases with increasing water depth. Due to the inherent spectral similarity amongst many species, including taxonomically dissimilar species, remote sensing underestimates biodiversity and represents the lower limit of actual species diversity.

The overall implication is that coral reef ecologists using remote sensing need to consider the spatial and spectral context of the imagery, and remote sensing scientists analyzing biodiversity need to define confidence limits as a function of both water depth and the scale of information derived, e.g., species, groups of species, or community level.

Keywords: coral reefs; remote sensing; field spectra; scale; ecology; biodiversity; conservation

1. Introduction

Remote sensing has become increasingly important among the fields of ecology, biodiversity, and conservation, appealing to scientists by providing repeat temporal observations over broad spatial scales and offering relative simplicity for acquiring data over large areas, as compared to extensive fieldwork [1–3]. Given numerous anthropogenic stressors, in conjunction with recent climate change, the species range and composition of various marine and terrestrial communities are rapidly declining [4–6]. Thus, rapid and repeatable assessment of coral reef ecosystems has become an important objective for monitoring the associated impacts of climate change on coral reef communities [7–10]. In this regard, remote sensing technologies provide valuable information related to the spatial analysis of ecosystem properties, including habitat composition, biodiversity, and the design of marine protected areas [11–13]. Further, the available remote sensing tools and analysis techniques are ever evolving, and new capabilities continue to emerge, including sensors with improved spatial and spectral resolution [3,10,14].

Hyperspectral remote sensing (imaging spectrometry) in particular shows strong potential for developing enhanced analysis tools to assess patterns and processes of reef composition and biodiversity [15–21]. However, to better leverage this technology, it is important to improve our understanding of the spectral characteristics and relationships of the various reef components. It is the variability in composition and structure of different components that manifests as variability in spectral reflectance, and inverting this relationship through image analysis facilitates the identification and classification of coral reef biota and substrates using remote sensing. Past research indicates that reef components can be differentiated according to general categories, e.g., live coral, carbonate sand, macroalgae, and seagrass [16,19–25]. This knowledge has assisted with the development of reef classification schemes, but further research is required to evaluate how the spectral variability between categories and within categories affects image-derived estimates of biodiversity.

Additional research is also required to identify and specify limits on our ability to differentiate species according to their spectral characteristics. More specifically, it has been shown that reef species can be generally categorized into a discrete number of categories [26] with many species exhibiting similar spectral characteristics. The inability to classify or distinguish distinct coral species as a function of spectral reflectance results because many coral species share a common suite of pigments that are conserved over geographic and taxonomic boundaries [22,27]. Additionally, only limited research has been conducted to examine how species separability, and hence detectability via remote sensing, changes with varying water properties and water depth (e.g., [28–30]). As such, detailed spectral

taxonomic classification and further environmental details are needed at appropriate spatial and temporal resolutions to improve ecological assessments (e.g., estimates of abundance, distribution, patchiness, and biodiversity) and better inform reef management decisions [2,8,12,31,32].

Numerous studies have successfully integrated fieldwork and various remote sensing techniques that have identified coral morphologies, habitat maps, live coral indices, coral reef resilience indicators, and other general reef categories [8,15,16,21,23,33,34]. Likewise, the ability to detect coral bleaching [35–38] and diseased states in corals [39], continues to improve with recent advances in remote sensing. Even so, coral reef managers are yet calling for an improved understanding of biodiversity (species) estimates derived through remote sensing [1,2,31]. Towards that end, it is necessary to further examine detailed spectral variability of the spatially dominant reef species (*i.e.*, those species that significantly contribute to the remote sensing signal), as well as analyze how inter- and intra-species spectral relationships vary as a function of environmental characteristics and water depth. Also of fundamental importance is determining the appropriate spatial scale for a given investigation as well as being able to effectively interpret and put that information in context across different spatial scales [34,40–43]. To objectively evaluate these requirements, locally optimized projects (*i.e.*, fine spatial scale reef habitat plots $\sim 5 \text{ m}^2$), where high spatial and high spectral resolution imagery (*i.e.*, hyperspectral) coincide with detailed *in situ* spectral measurements and ecological field data, are needed to assess the spectral processes that reflect the composition, distribution, and biodiversity found on coral reefs.

The objective of this study is to provide a broader understanding of reef spectral variability and the effect of depth on our ability to distinguish species, groups of species, or even major reef components (*i.e.*, sand, algae, seagrass, dead coral, live coral). We also aim to invoke further discussion and additional research on the relationships between spectral diversity and species diversity. Here we describe methods that provide the opportunity to correlate spectral characteristics with localized *in situ* measurements of biodiversity (species) that can be scaled-up to the spatial resolution and geographic extent provided through remote sensing image analysis. Specifically, the goals of this study are to: (i) identify the spectral characteristics of the spatially dominant taxa for a coral reef system in southwest Puerto Rico; (ii) assess the ability to differentiate species based on spectral characteristics; and (iii) examine how spectral separability and varying water depth impact our ability to estimate biodiversity and classify species, or groups of species, using remote sensing data.

2. Materials and Methods

To evaluate spectral characteristics of different species and different groups of species, an extensive sample of *in situ* spectral measurements were acquired from the spatially dominant reef and seagrass species in southwestern Puerto Rico. A semi-analytical algorithm for the water column was next used to model the influence of increasing water depth on the average spectral reflectance of each species. The resulting spectra at each depth were then grouped according to spectral similarity using hierarchical clustering. In the same study area, corresponding photoquadrats were collected from small habitat plots and visually analyzed to determine field estimates of biodiversity. These field estimates were then recalculated at each depth using the results of the spectral clustering analysis to demonstrate the influence of increasing water depth and spectral similarity on remote sensing derived biodiversity.

2.1. Reef Field Spectra

Field reflectance spectra were collected *in situ* from amongst the inner shelf reefs of southwestern Puerto Rico, focusing predominantly on Enrique Reef, using a GER-1500 spectrometer in an underwater housing with attached illumination source (Spectra Vista Corporation, Poughkeepsie, NY, USA; Figure 1) [44,45]. The GER-1500 measures 512 spectral bands from 350 to 1050 nm at a 1.5 nm sampling interval. The unit is self-contained and can be easily operated using external controls on the underwater housing. The attached quartz halogen light provided steady, spectrally consistent, light with which to acquire measurements, and thus effectively eliminated uncertainties associated with the inherent variability of the natural underwater light environment. Field methodology followed standard spectral collection protocols, where target measurements of species and substrate were normalized to reflectance using contemporaneous *in situ* reference measurements of a 99% Spectralon panel (Labsphere, North Sutton, NH, USA). Included in the final data were measurements of 40 different marine species, representing Cnidaria, Porifera, and submerged aquatic vegetation (e.g., seagrass and algae), as well as representative samples of numerous sand areas. The resulting coral reef spectral library was organized by taxa, size, and spatial dominance, and cataloged using SAMS (Spectral Analysis and Management System) [46]. Data was analyzed to calculate the mean and standard deviation for each individual species plus sand, resulting in representative reflectance spectra for 41 different reef components.



Figure 1. The GER-1500 spectrometer in underwater housing with attached illumination (left) and a map of the study location off the coast of southwestern Puerto Rico (right).

2.2. Separability Analysis and Water Column Modeling

Measured field spectra represent reflectance at zero water depth, where the artificial illumination and reference Spectralon measurements serve to effectively remove influences of varying water properties, fluctuating natural light, and differing water depths. While useful for *in situ* spectral analysis and remote sensing studies with robust water column correction schemes (which are difficult

to achieve and not typically the norm), it is informative to investigate how the water column influences spectral relationships at different depths.

To introduce a simulated water column to the average reflectance spectra for each of the measured 41 reef components, water column modeling was performed using the semi-analytical algorithm developed by Lee *et al.* [47,48]. This is a widely-accepted model in the remote sensing community that is commonly used as an “inverse” model to derive coastal water properties from hyperspectral imagery [17], whereas here it is used in an equally applicable role as a “forward” water column model. Here the model is used as a discrete example of how the water column can influence spectral characteristics at the water surface; however, analysis could also be adapted to other water properties, models and measurements, or extended to also consider the additional confounding impact of variations in water properties. In this study, a set of default values were used to parameterize the model for clear tropical water: phytoplankton absorption at 440 nm = 0.05 m^{-1} ; detritus/gelbstoff absorption at 440 nm = 0.05 m^{-1} ; and particle backscattering at 440 nm = 0.01 m^{-1} . Output from the model, which was replicated at 1, 3, 5 and 10 m water depths, represents reflectance spectra at the water surface (*i.e.*, as if viewing each reef component through the water column).

A quantitative analysis was used to calculate the similarities and differences, and thereby assess the ability to spectrally differentiate, between the various reef components at each depth. The metric selected for quantifying the level of separability was spectral angle, which calculates the “angle” between two spectra in n -dimensional space [49]. The smaller the angle, the less separable two spectra are considered. Spectral angle was calculated pairwise at each depth (0, 1, 3, 5 and 10 m) for all possible combinations of reef components. A weighted hierarchical clustering scheme (cluster distance is the average distance of pairs between each cluster weighted by number of members in each cluster [50]) was next used to generate optical dendrograms (as opposed to taxonomic) that define how components are progressively grouped as a function of increasing spectral angle.

2.3. Field Estimates of Biodiversity

To correlate the spectral analysis with reef composition and biodiversity, photoquadrat images were obtained from selected habitat plots on Enrique Reef. Photo acquisition coincided with a 2013 airborne hyperspectral mission conducted over the same area, which is being used in a related project to investigate and develop remote sensing estimates of biodiversity. The particular study location, Enrique reef, is an important component of the CenSSIS-SeaBED project [51], where over the last decade UPRM researchers have compiled an extensive array of image and field data as support for testing and validating remote sensing algorithms for benthic habitat mapping. Habitat types on Enrique Reef include large areas of seagrass, patches of pure carbonate sand, and a diverse coral reef community including areas of both hard and soft coral. The reef measures approximately $1 \times 0.5 \text{ km}$, and includes water depths ranging from $>10 \text{ m}$ along the fore and back reef, 1–3 m along the reef flat, and $<1 \text{ m}$ along the reef crest, with areas of exposed sand and rubble and emergent mangroves.

Photoquadrat images were obtained from selected plots within the seagrass ($n = 44$) and coral reef ($n = 26$) habitat areas on Enrique Reef. For each habitat plot, a $1 \times 1 \text{ m}$ quadrat was randomly placed five times within a 2 m distance around a central point (marked with buoys), acquiring high quality photographic images of each quadrat location using a Nikon P7000 digital camera (Figure 2). The five

photoquadrats sampled for each plot were used to statistically represent the 4 × 4 m (16 m²) habitat characteristic for each plot. Individual plots were randomly located within each habitat type a minimum distance 10–15 m apart, and a Magellan Mobile Mapper 6 GPS was used to record the central location of each plot.



Figure 2. (a) Flagged rebar was hammered into non-living substrate and tightly tethered to the surface to mark the GPS location for each habitat plot; (b) Photoquadrat of seagrass area mixed with soft corals; (c) Photoquadrat of from the reef crest area showing soft corals, hard corals, encrusting sponge, algae and non-living substrate; (d) Recording the GPS location of a habitat plot (tethered buoy).

Summary statistics of habitat composition were derived from each group of five photoquadrats for each plot (pooled photoquadrats) using on-screen visual classification and identification [52,53]. The resulting statistics were used to calculate diversity using the Shannon Weiner Index, where the exponential of Shannon entropy [54,55], “diversity of order one”, was utilized to provide meaningful comparisons of biodiversity across this single marine landscape (inclusive of seagrass beds, sand patches, and coral communities). Considering that estimates of alpha diversity (habitat) and beta diversity (extent of differentiation among those habitats) [54] are independent, the exponential of Shannon entropy accounts for all species according to frequency, and rare or common species are not favored disproportionately, therefore making it the “fairest” index for the purposes of differentiation among the given coral reef habitats (Equation (1)):

$${}^1D = \exp\left(-\sum_{i=1}^R p_i \ln(p_i)\right) = \exp(H') \quad (1)$$

where 1D is diversity of order one, p_i is the relative proportion of species i relative to the total number of species R , and H' is the Shannon index value calculated using natural logarithms [55].

Utilizing results from the separability analysis, which provided an indication of how reef components group together spectrally (not taxonomically), calculations of the Shannon index were repeated for different water depths using the indicated spectral groupings. In other words, wherever analysis revealed certain species could not be reasonably differentiated spectrally, these species were grouped together and the Shannon index was recalculated with a reduced number of total “species”. Using output from the hierarchical clustering scheme at each depth, species were deemed spectrally inseparable if the spectral angle was <0.1 ; and conversely, separable if the spectral angle was ≥ 0.1 . The 0.1 threshold is a common default value in spectral analysis; however, the threshold could be adjusted to reflect the specific variability of any given spectral dataset. The separability analysis allowed field measurements of biodiversity to be adapted to the remote sensing perspective, demonstrating how spectral characteristics influence what can be resolved in remote sensing imagery.

3. Results

3.1. Reef Field Spectra

A total of 9400 *in situ* spectra samples (after removing erroneous or noisy spectra) were collected from 41 reef components in five categories: hard corals, soft corals, sponges, submerged aquatic vegetation (SAV; *i.e.*, seagrass and algae), and carbonate sand (Table 1; Figures 3 and 4). Not intended to be inclusive of all species in the study area, these components represent a comprehensive sampling of those species that are individually or aggregately sizeable enough to contribute significantly to the remote sensing signal. Hence, these components also represent the feasible upper limit of taxonomic detail that can be achieved for remote sensing of biodiversity in this area.

Table 1. Summary of field reflectance spectra (R) collected from shallow reef areas in southwestern Puerto Rico. Instrument configuration was set to automatically record and average four samples for each measurement.

Phylum	Individuals	Species/Type	Samples	Spectra R
Cnidaria	73	25	5556	1389
Porifera	34	11	2028	507
SAV (seagrass/algae)	Numerous	4	1268	317
Sand/Substrate	Numerous	1	548	137
Totals	107	41	9400	2350

The individual reflectance spectra exhibit smooth curves with negligible noise from 400 to 800 nm, demonstrating the advantages of using artificial light. More specifically, given the challenges of acquiring *in situ* underwater measurements using natural sunlight, which are susceptible to fluctuations in the incident downwelling light (e.g., associated with light refraction, wave focusing, variable wave height, and instrument and diver self-shading), utilizing artificial light minimizes the uncertainty associated with these unwanted natural light variations. As a result, observed variations in spectra can be confidently attributed to actual physical variations in species and substrate reflectance characteristics.

Figure 3 illustrates an example subset of spectra acquired from a single coral species (*A. palmata*), where it is evident that while variability exists within the individual measurements for this species there is also a strong degree of similarity. Considering that similar relationships are observed amongst all of the measured species (Figure 4), this indicates that spectral similarities can exist both within and between different species.

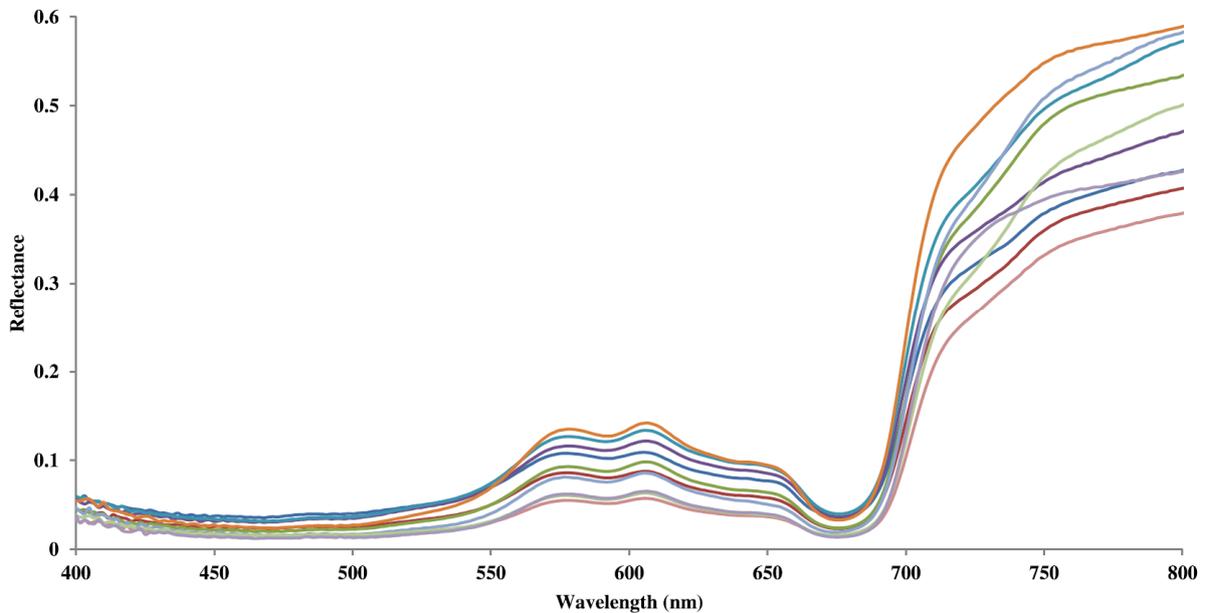


Figure 3. Representative individual spectra measured for *Acropora palmata*; examples shown here are 10 spectra subset from a total sample size = 139 spectra.

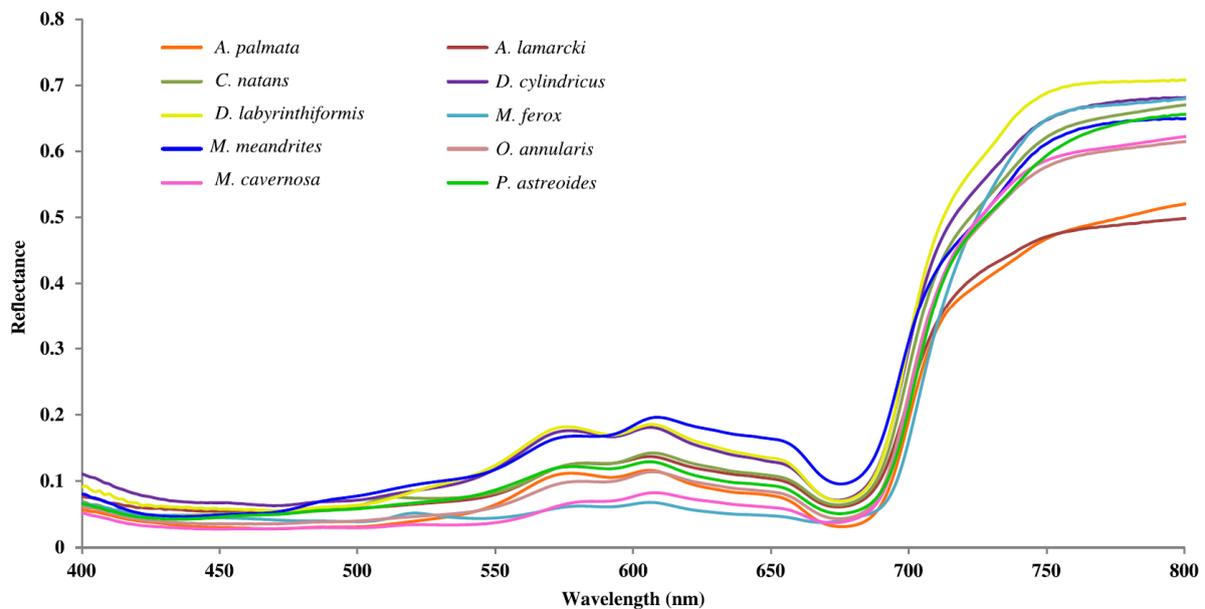


Figure 4. Representative average spectra for ten coral species; examples shown here are subset of the 25 total Cnidarian species sampled (5556 samples; 1389 reflectance spectra).

3.2. Spectral Separability

Analysis of spectral separability, and correspondingly spectral similarity, was performed at two different taxonomic levels: (i) as groups of related species; and (ii) ungrouped as individual species. Calculations were performed using 38 of the 41 measured components, eliminating those with fewer than 10 spectral measurements and thereby retaining only those components with sufficient sampling to be considered representative of each species' reflectance characteristics.

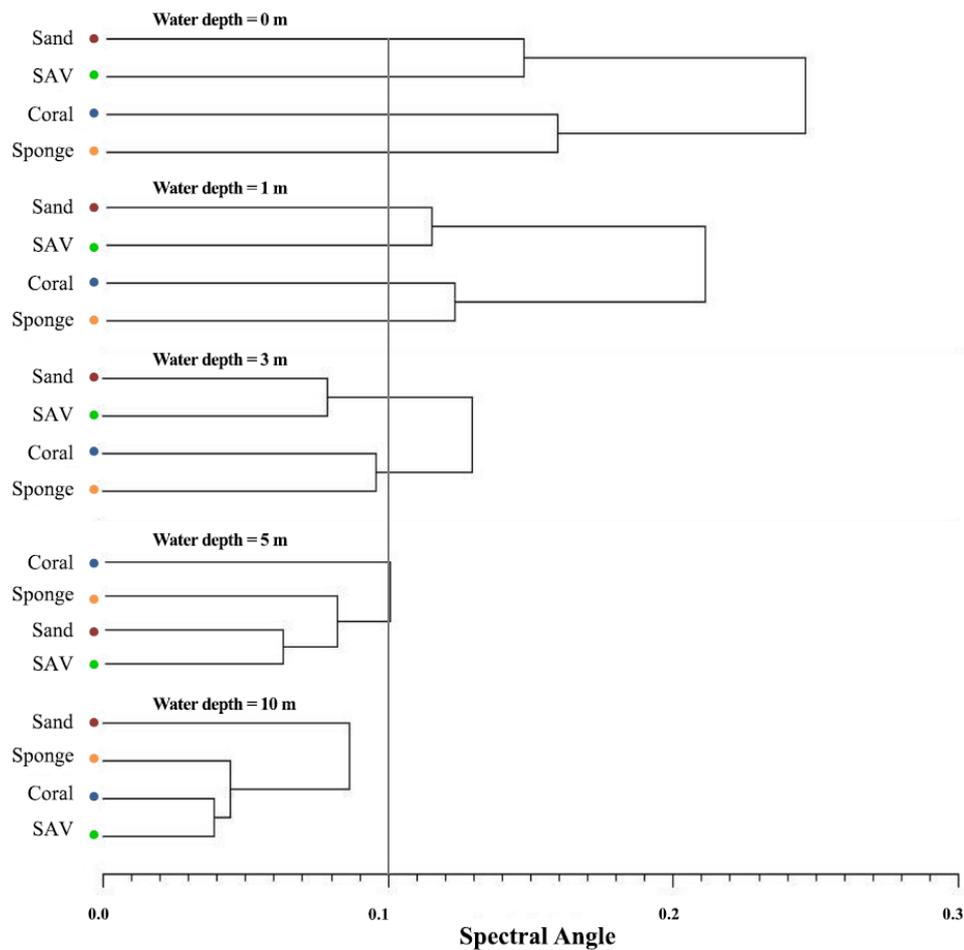


Figure 5. Optical dendrograms illustrating the effect of increasing depth on separability of field spectra grouped into four fundamental reef components: coral, sponge, submerged aquatic vegetation (SAV), and sand.

The first level of analysis grouped the reef spectra into four fundamental components: coral, sponge, submerged aquatic vegetation (SAV), and sand. Average spectra were generated, and results were used to calculate spectral angles between the components as well as generate optical dendrograms for each of five water depths: 0, 1, 3, 5 and 10 m. Using a reasonable spectral angle threshold of 0.1 it is evident that the average *in situ* field spectra of these components exhibit unique reflectance characteristics and can be readily differentiated at 0 and 1 m water depth (Figure 5). However, with increasing water depth the relative separability of these four components decreases. For example, even when considering a lower spectral angle threshold, it is more difficult to differentiate sand from SAV and coral from sponge at 3 m water depth, and at 10 m water depth the system is

essentially reduced to two differentiable components: sand vs. coral, sponge and SAV (Figure 5). It is also instructive to observe that the hierarchical relationships can change with depth (e.g., SAV is most closely grouped with sand up to a depth of 5 m and then shifts to coral as its closest spectral component at 10 m), an observation that is even more apparent in the results that follow for the individual species.

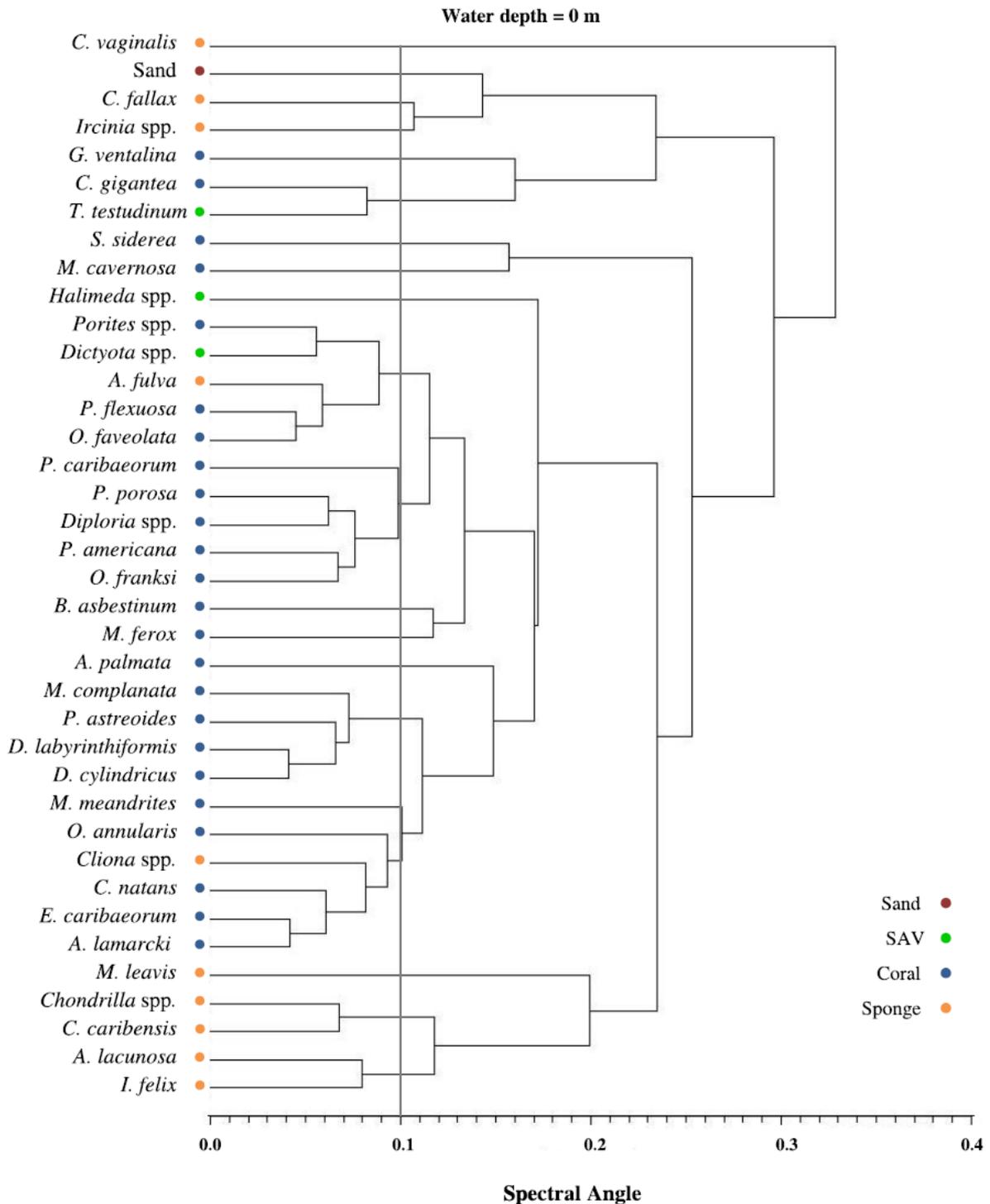


Figure 6. Optical dendrogram for 0 m water depth illustrating separability of field spectra from 24 coral species, 10 sponge species, 3 submerged aquatic vegetation (SAV) species, and sand.

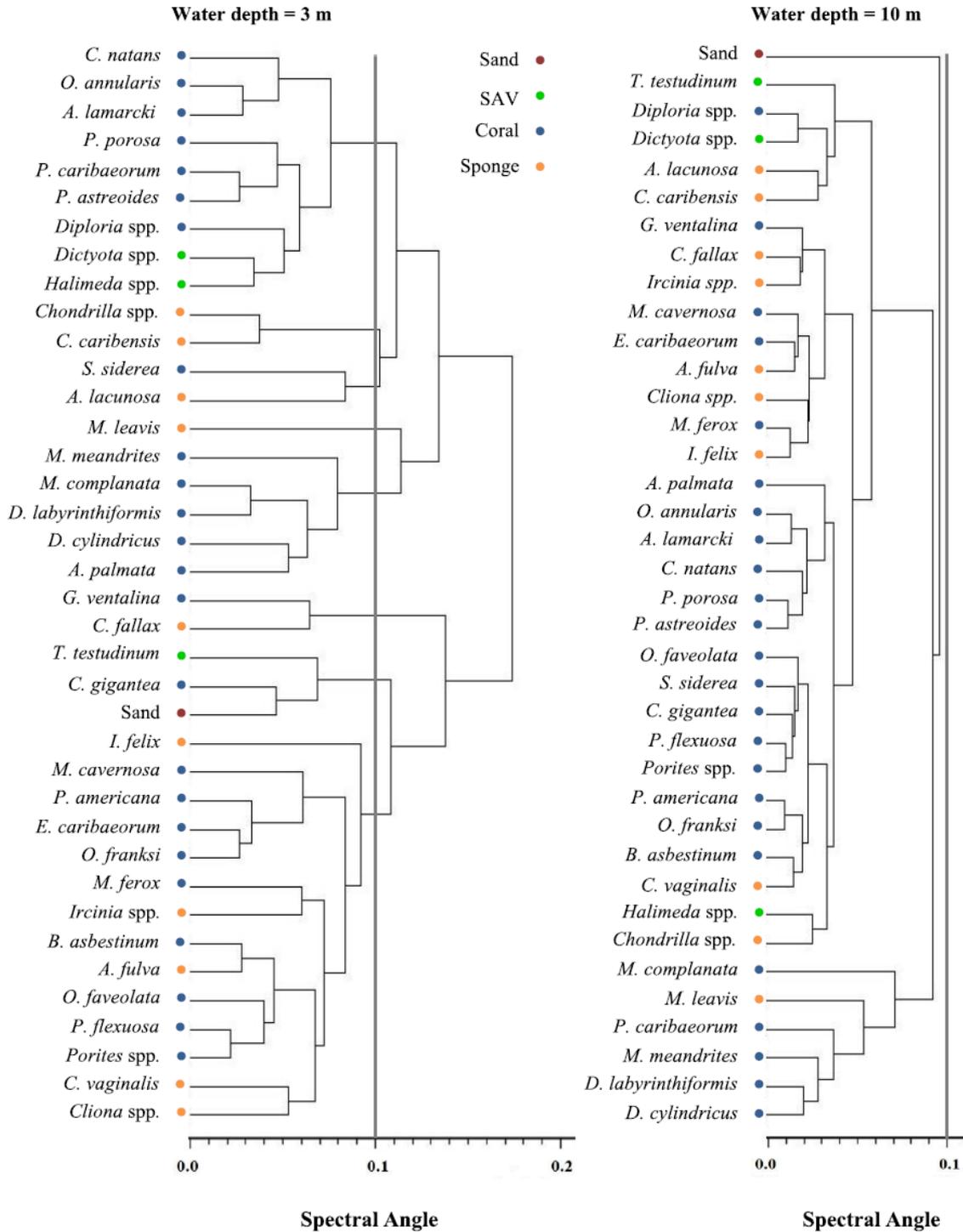


Figure 7. Optical dendrograms for 3 and 10 m water depth illustrating the effects of increasing depth on separability of field spectra from 24 coral species, 10 sponge species, 3 submerged aquatic vegetation (SAV) species, and sand.

When applying the same pairwise spectral angle calculations and optical dendrogram creation using the average individual spectra, results reveal that even at 0 m water depth there are already many species that are difficult to separate spectrally (Figure 6). In some cases species group together within categories, such as coral with coral (e.g., *D. labyrinthiformis* and *D. cylindricus*), but in other cases species are grouped outside their respective categories, such as coral with algae (e.g., *Porites* spp. and

Dictyota spp.). While biologically different, this spectral similarity across categories may be explained by the presence of common photosynthetic pigments between species. For example, Hochberg *et al.* [56] and Torres *et al.* [57] both provide evidence that certain corals contain the same pigments (e.g., carotenes and xanthophyll) that also characterize brown algae. When the effects of the water column are included, the ability to distinguish individual species diminishes significantly with increasing water depth (Figure 7). [Note: for brevity only the optical dendrograms from 3 and 10 m water depth are displayed here]. Furthermore, varying water depth is also accompanied by substantial variations in how spectra are grouped, regardless of taxonomic relationship. For example, *Dictyota* spp. is most closely grouped with *Porites* spp. at 0 m depth, whereas at 3 m it is grouped with *Halimeda* spp. and at 10 m it is grouped with *Diploria* spp. These changing spectral relationships are attributed here to the inherent nonlinearity of light interaction and attenuation in the water column; but when also considering intra-species spectral variations these relationships can be further influenced by depth dependent differences in photosynthetic pigment content within species [58]. This indicates that unless such variations are accounted for, significant uncertainty can be associated with species-level spectral and image analysis. Furthermore, considering the correlation between increasing depth and decreasing spectral separability, these results also affirm the importance of compensating for variable water depth (e.g., using a depth invariant index, semi-analytical algorithm or radiative transfer model) when deriving habitat classifications and biodiversity estimates using remote sensing.

3.3. Field Estimates of Biodiversity

Photoquadrats were acquired from a total of 90 plots distributed across three different habitat categories: coral reef community ($n = 26$), dense seagrass ($n = 44$), and pure sand ($n = 20$). As expected, field estimates of biodiversity derived from photoquadrats using the Shannon index (order one diversity) $\exp(H')$, revealed different magnitudes of biodiversity corresponding to each of the three habitat areas. Estimates ranged from no biodiversity $\exp(H') = 1$ in areas of pure carbonate sand, low/moderate diversity $\exp(H') = 1-3$ in seagrass areas, and high biodiversity $\exp(H') = 10$ in reef communities. After using results from the separability analysis to group spectrally similar species and recalculate the Shannon index for different depths, it is observed that estimated biodiversity, as well as the range and standard deviation, decreases with increasing water depth (Figure 8). This indicates that depth-influenced estimates of biodiversity derived from remote sensing (*i.e.*, optical diversity) can significantly underestimate biodiversity and represents the lower limit of actual species diversity. For example, depending on water depth, species composition, and the associated spectral relationships, a hypothetical optical diversity index of 1 for seagrass could indicate an actual biodiversity index of 1-3, whereas an optical diversity index of 1 for coral could indicate a biodiversity index as high as 10. Based on this analysis, it appears feasible to derive mathematical relationships for each habitat type that correlate optical diversity with biodiversity as a function of water depth, and then utilize these empirical functions to normalize remote sensing derived estimates of biodiversity. Although implementation of such a technique would require knowledge of water depths for a given study area, these values are often available from bathymetric charts or can alternatively be estimated directly from the imagery.

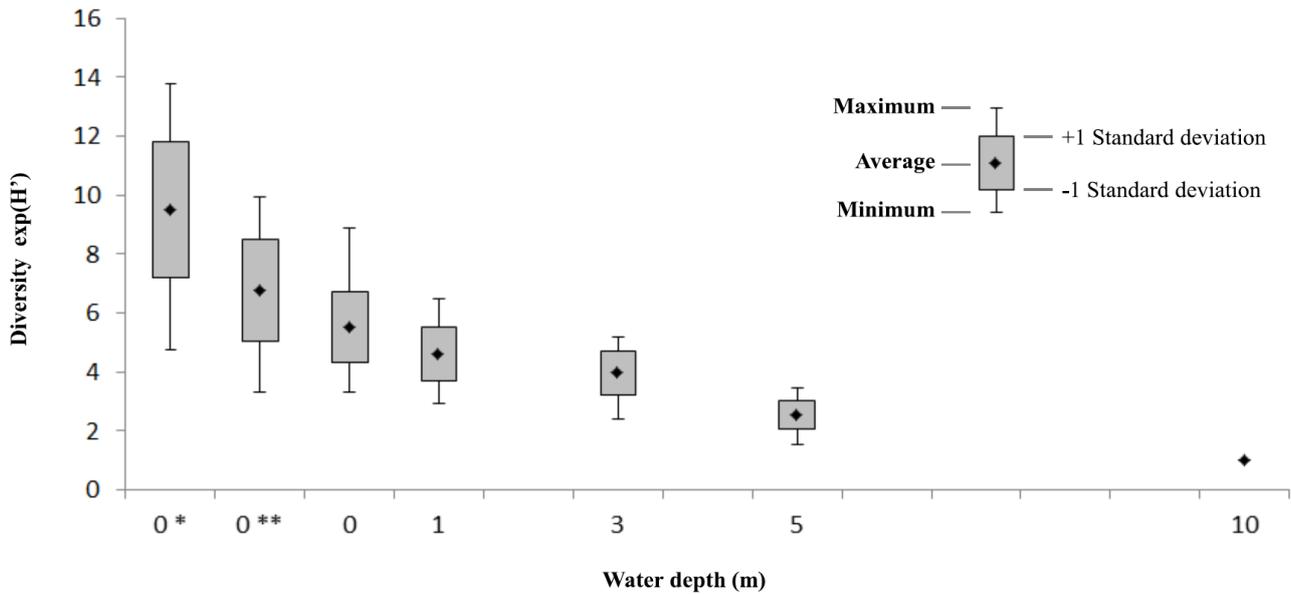


Figure 8. Estimates of biodiversity calculated using the exponential of Shannon entropy, $\exp(H')$, illustrating influence of increasing spectral similarity amongst reef species as a function of increasing water depth: 0* is biodiversity obtained from photoquadrats, 0** is biodiversity calculated using only those species considered prevalent or sizable enough to significantly influence the remote sensing signal (*i.e.*, species included in the spectral measurements for this study area), and 0–10 is biodiversity calculated with consideration for optical similarities amongst species (*i.e.*, based on hierarchical clustering of reflectance spectra as influenced by the overlying water column).

The overall results of this investigation suggest three important implications for remote sensing of biodiversity: (i) unless the influence of the water column is accounted for, then estimates of biodiversity for any given area will be depth-biased; (ii) given the occurrence of spectral similarity amongst reef species, even without influence of the water column, biodiversity estimates should not be considered absolute but rather the minimum or lower limit of true biodiversity; and (iii) even small or moderate differences in remote sensing derived optical diversity may indicate substantial differences in actual species diversity.

4. Discussion

This study explored spectral relationships of reef components in southwestern Puerto Rico and illustrates how the overlying water column can impact these relationships. Results indicate that the ability to distinguish individual species significantly diminishes with increasing water depth, thereby contributing a level of uncertainty to any spectrally derived estimates of biodiversity, such as through remote sensing. Additional considerations not addressed in this analysis, but that would contribute further uncertainty, include: variable water properties and water surface conditions, differing sensor spectral and spatial characteristics, within-species spectral variations, and overly simplified or imperfect water correction schemes. Thus, it is expected that the observations illustrated here for Puerto Rico would be equally applicable to reef remote sensing elsewhere around the globe. So, if species level distinctions are not feasible with remote sensing imagery, then what can be detected in a

remote sensing pixel? At what level can biodiversity be measured? Moreover, can a biodiversity index for coral reefs be conceived using remote sensing? And if so, how do we correlate spectral diversity measured in remote sensing with biodiversity and reef composition values generated from field data? The answers to these questions lie in continuing to improve our understanding of the complex relationships and environmental drivers that govern species distribution, continuing to investigate relationships between optical diversity and species diversity, and utilizing this knowledge to improve our capacity for monitoring biodiversity using remote sensing imagery.

Remote sensing is a powerful tool for assessing reef characteristics over large spatial areas, including the estimation of biodiversity, but interpretation of image-derived output requires informed decision making from remote sensing specialists and ecologists alike regarding physical constraints on what is being measured and what the confidence levels are for those measurements. An important aspect of consideration for remote sensing users and producers is to understand the scale of observation, inclusive of spatial extent, observation detail, and taxonomic level. For example, the *Pyramids of Observation* illustrate the different scales and relationships that exist in remote sensing and field-based studies of biodiversity (Figure 9).

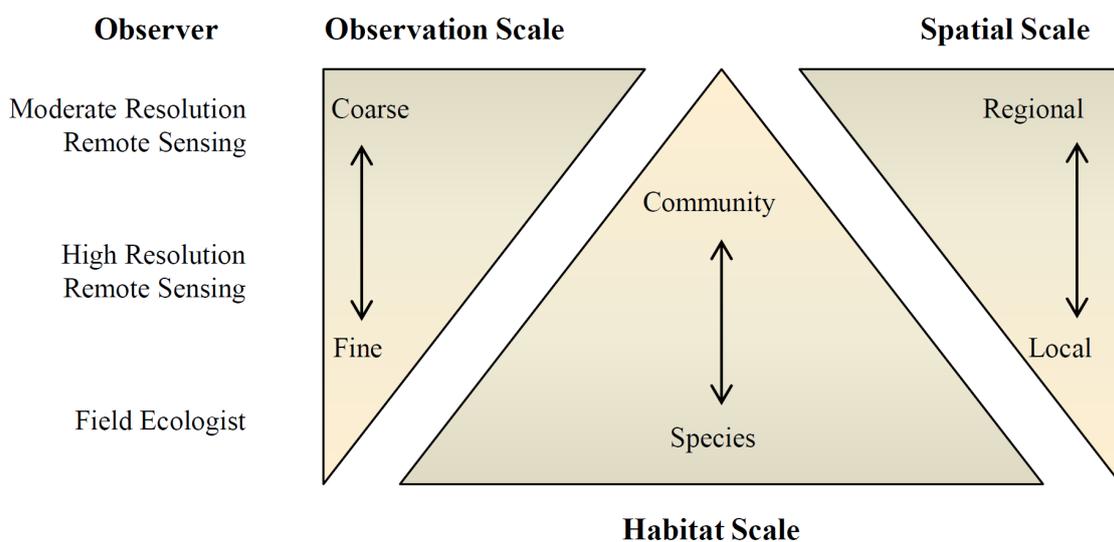


Figure 9. The *Pyramids of Observation* relating the different scales at which biodiversity is measured from the perspective of both remote sensing and field-based analysis.

The lower levels of the pyramids represent the finest scale of observation, such as where the marine field ecologist records detailed habitat information and species composition within a local study area. Moving up through the pyramids depicts decreasing levels of habitat information acquired at a coarser observation scale, but with increasing magnitude in spatial coverage. Remote sensing is represented at two levels within the context of these pyramids: high resolution (<5 m pixel scale, e.g., WorldView-2) and moderate resolution (5–100 m pixel scale, e.g., Landsat). A caveat here is that the distinction between moderate and high-resolution spatial coverage is becoming more a function of processing capacity, and less an issue of acquisition extent, as more and higher resolution imagery becomes available globally. In this situation, even with high spatial resolution imagery (e.g., 30 cm WorldView-3) the primary challenge remains overcoming radiometric and spectral resolution. Nonetheless, increasing from moderate to high resolution remote sensing facilitates detection of an

increasing number of general habitat categories, such as differentiating more variations in seagrass density and coral community type. However, as shown here, except for situations where certain species exhibit unique spectral characteristics, even with high spectral, high spatial resolution imagery it is currently not possible to spectrally differentiate all individual species. This constraint is a function of both spectral similarity amongst species and spatial size or extent, where many species are not prevalent or sizable enough to significantly influence the remote sensing signal. This in turn has direct relevance to remote sensing estimates of biodiversity, which become inherently limited by these spectral characteristics. For example, a large expanse of seagrass can appear as a relatively uniform dark area in moderate resolution imagery and as a collection of different seagrass densities in high resolution imagery; however, a field ecologist surveying the same area can identify a patchy distribution of numerous benthic groups and species, such as scleractinian corals, octocorals, sponges, macroalgae, and even different seagrass species. In other words, there is typically an intrinsic tradeoff between the scale of observation and the scale of information.

To better understand the implications of this observation tradeoff there is a need to more explicitly define the relationships between optical diversity and species diversity. A common challenge when linking remote sensing applications and coral reef ecology is the calibration and validation of field data with data from remote sensing imagery [21], especially in marine environments [59]. For example, field data and remote sensing image acquisitions are not always coincident [7,8,21,60], and in some cases there are even years of difference between the acquisition of field and image data [8,60]. Additionally, spectral libraries for marine species remain undersampled, and significant opportunity exists for detailed analysis of intra- and inter-species similarities. As such, while there are many informative coral reef remote sensing applications, there is yet a need for more studies that incorporate specific consideration for calibrating and validating remote sensing estimates of biodiversity. This includes directly correlating small-scale localized field estimates of biodiversity and species composition in different habitat areas with estimates derived from corresponding high spectral, high spatial resolution imagery. It is also instructive to consider information and measurements derived from other related disciplines, such as climate patterns, physical processing, ocean chemistry, larval dispersal and population connectivity, which can further contribute to the overall assessment of biodiversity [1,31,61]. Once the variability in spectral diversity is better understood at these scales, it then becomes feasible to extend the observed correlations to other spatial and spectral scales, and thereby develop more effective tools for linking remote sensing biodiversity estimates with field ecology.

5. Conclusions

This study demonstrated that although average field spectra can be used to differentiate many coral reef species, once the overlying water column is considered the ability to distinguish species significantly declines with increasing water depth. These results illustrate the challenges associated with developing a depth-invariant biodiversity index using remote sensing, and reveal that there is important groundwork ahead for reef ecologists and remote sensing specialists to better understand the relationships between optical diversity and species diversity.

Remote sensing will no doubt continue to serve as an important tool for ecology, conservation, and biodiversity, particularly considering the current predictions of continued environmental degradation related to climate change on a global scale. Consequently, it is imperative that we continue to improve our abilities for rapid ecological monitoring using remote sensing, including the capacity to assess and monitor changes in coral reef biodiversity. As remote sensing technologies improve in both coverage and resolution (spatially, spectrally and temporally), there is increasing opportunity, given development of a strong foundation in spectral knowledge, to realize these improvements and put the resulting analysis tools into practice.

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Author Contributions

Both authors contributed equally to this work. M.L. collected the spectral library; M.L., J.G. analyzed field spectra; M.L. performed fieldwork and biodiversity estimates, J.G. performed spectral endmember analyses and generated dendrograms. M.L. and J.G. wrote the paper.

Conflicts of Interest

The authors declare no conflict of interest.

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