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# Predicting spatial patterns in intertidal seaweed habitats using remote sensing and hierarchical species community modelling

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## ABSTRACT

Remote sensing of intertidal seaweed habitats is challenged by overlapping spectral signals from multiple co-occurring species groups, making it difficult to predict their distributions. This study applies Hierarchical Modelling of Species Communities (HMSC), a joint species distribution framework that accounts for statistical dependencies and co-occurrence patterns among species groups, thereby improving prediction accuracy, particularly for groups that are otherwise difficult to model individually. We tested this approach using Sentinel-2 (S2) satellite imagery to estimate the coverage of green, brown, and red algae along the Veraval coast, Gujarat, India. To assess whether the findings could be reproduced beyond the original study area, we repeated the joint-versus-single-group comparison using a larger, spatially independent regional dataset from the Saurashtra and Gulf of Kachchh coasts of Gujarat. The HMSC framework effectively modelled the simultaneous distribution of green and red seaweeds based on their shared and individual responses to covariates derived from remote sensing data. Brown algae were weakly predicted at Veraval, where they were sparsely represented, and remained less predictable in the Saurashtra and Gulf of Kachchh dataset despite their higher occurrence and cover, suggesting limited spectral separability, within-group optical heterogeneity and mixed-pixel effects rather than insufficient representation alone. Still, the results show that this method is a promising tool for monitoring complex shallow coastal habitats at local scales and may support ecosystem assessment and management when applied within its demonstrated domain.

## Introduction

Intertidal ecosystems are important biodiversity hotspots, characterised by rich benthic habitats that provide crucial functions to their surrounding marine environments (Schenone and Thrush 2020). Their proximity to human activity makes them important providers of ecosystem services by offering opportunities for recreation and education and supporting key ecological benefits such as nutrient cycling (Barbier et al. 2011). However, this proximity also exposes these habitats to significant anthropogenic pressures, often increasing their vulnerability and degradation (Portugal et al. 2016; Aps et al. 2018). The intrinsic mosaic nature of these habitats can mask anthropogenic effects, as traditional sampling methods are often inadequate to capture their complex spatial heterogeneity or to offer early warning of detrimental habitat changes. The task becomes even more daunting in remote regions where scientific

efforts may be sparse or non-existent. A comprehensive understanding of these habitats therefore requires innovative mapping methods that can accurately depict the current state of these ecosystems and monitor their temporal trends. Effective monitoring is essential for the development of appropriate conservation and management strategies, which is important not only to the scientific community but also to conservationists, policymakers, and other stakeholders concerned with the preservation of these marine assets (Maes et al. 2012; Seidel et al. 2019).

Remote sensing (RS) is a valuable tool for large-scale ecological mapping, providing a bird's-eye view of habitats that can be difficult to study using traditional field methods (Kutser et al. 2003; Pham et al. 2019). However, RS often involves trade-offs: broad, landscape-scale coverage may come at the expense of precision and detail compared to more localised, high-resolution analyses. Instrumentation plays a crucial role in defining what ecological features can be detected (Kutser et al. 2003). Key factors include the size of the pixel (spatial resolution) and spectral resolution of the sensor. The spectral resolution of instruments ranges from simple red–green–blue (RGB) imagers to multispectral and hyperspectral detectors, each with their own advantages and disadvantages. RGB satellite instruments provide basic colour information but often with high spatial resolution (1–3 m, e.g. WorldView, Pléiades, GeoEye, IKONOS, Dove) or with long data series allowing climate change studies (e.g. Landsat data series since 1984 with 30 m resolution). Hyperspectral sensors offer a wealth of detailed spectral information (Kutser et al. 2003, 2006) but mostly from airborne sensors such as CASI, AISA, HySpex, and many others. Hyperspectral satellite sensors have been scarce – Hyperion was launched in 2000, PRISMA in 2019, and EnMAP in 2022, with several others following later. Moreover, all the sensors had a 30 m spatial resolution, which is not sufficient in spatially very heterogeneous environments, as well as limited spatial and temporal coverage.

Despite these capabilities, relying on RS alone for benthic algal mapping presents significant challenges. First, recognition of different benthic types depends on the optical properties of these habitats. Second, the limitations come from the technical characteristics of each sensor (spectral and spatial resolution, signal-to-noise ratio, etc.), and third, the detail of benthic maps (number of benthic classes) derived depends on the method used. If the benthic habitats are submerged, then the main limiting factor for RS is water, which absorbs light very strongly in the red to infrared part of the spectrum, where the differences between benthic algae occur (Kutser et al. 2003). For example, red and brown macroalgae are spectrally separable from each other when they are out of water and hyperspectral sensors are used (Kutser et al. 2003), but either 1–2 m of water or the use of multispectral sensors lacking appropriate spectral bands makes this distinction impossible. In complex intertidal habitats, however, multiple algal taxa often co-occur within the area of a single satellite pixel, yielding mixed reflectance signals. Studies have shown that any level of sub-pixel mixing of benthic organisms can drastically reduce classification accuracy (e.g. overall separability drop-

ping below 60% when coral and algae co-occur within pixels) (Hedley et al. 2012). This mixed-pixel problem means that mapping algorithms that treat each pixel as one class may misrepresent the true mosaic of algal communities. More details about the limiting factors of spectral and spatial resolution of remote sensing sensors, as well as the methods used (from simple band ratios and supervised classifications to analytical methods using hyperspectral data and radiative transfer modelling), can be found in a shallow water remote sensing review paper by Kutser et al. (2020).

Furthermore, conventional RS methods (e.g. those described in Kutser et al. 2020) generally model target classes independently and do not explicitly use residual associations or co-occurrence structure among algal groups. Such associations can contain predictive information, although they should not be automatically interpreted as causal biotic interactions. In summary, a purely RS-based image-classification approach (even using modern machine learning) faces inherent disadvantages: it requires extensive training data for each benthic class, cannot easily handle multi-species mixtures in pixels, and may fail to exploit ecological relationships among taxa.

To overcome these gaps, we combined RS with a multivariate statistical modelling approach. The cohabitation of target species with other species or groups can influence the reflectance values recorded at a site, introducing significant among-species residual correlation (analogous to spatial or temporal correlation in single-species studies). Mapping the coverage of all algal groups within a single, joint framework accounts for residual associations and shared environmental responses. Therefore, a modelling algorithm capable of handling such multivariate complexity is essential to enhance the effectiveness of algal mapping from remote sensing data. Hierarchical Modelling of Species Communities (HMSC) is one such framework – a Bayesian multivariate statistical approach that integrates species occurrence or abundance data with environmental covariates (Ovaskainen et al. 2017). This enables the simultaneous modelling of multiple species while accounting for their co-occurrence patterns and dependencies on environmental variables (in our case, the spectral signals from remote sensing). The hierarchical structure of HMSC allows for partitioning the variation in species occurrences into components driven by environmental filtering, species associations, and random processes, facilitating inferences at both the species and community levels (Ovaskainen et al. 2017). HMSC has demonstrated strong predictive capabilities, even with sparse data, by effectively ‘borrowing strength’ across species (Norberg et al. 2019). Recent advancements have significantly improved the efficiency of HMSC model fitting, enabling the analysis of large and complex datasets (Rahman et al. 2024). Notably, joint species distribution models such as HMSC have been applied in various ecosystems worldwide to improve biodiversity predictions by accounting for co-occurrences (Pollock et al. 2014; Warton et al. 2015), thereby overcoming a major limitation of single-species models that ignore interspecies relationships (Pollock et al. 2014). For these reasons, HMSC is a powerful tool for ecologists: it helps predict and describe multivariate associations within species communities and their links to environmental covari-

ates such as RS data, although it has not yet been applied in RS contexts. By integrating satellite RS, in situ observations, and the HMSC algorithm, this approach has the potential to produce scalable biodiversity maps and assess ecosystem trends across multiple species, once supported by sufficiently rich training data (Kerry et al. 2022). Continued refinement of these techniques is crucial to ensure their adaptability and effectiveness in addressing the complexities of global ecosystems (Araújo and Peterson 2012; Jetz et al. 2012).

The present study was designed as a proof-of-concept application of HMSC. We first used Sentinel-2 (S2) imagery to examine relationships between spectral signals and the field-measured percentage cover of green, brown, and red algae along the Veraval coast of Gujarat, India. To evaluate the potential benefit of modelling algal groups simultaneously, we compared joint and single-group HMSC models fitted with the same predictor set, response distribution, spatial structure, HMSC settings, and five-fold cross-validation design. We then used the joint model to predict the spatial distribution of algal groups within the Veraval study area, restricting predictions to intertidal habitats comparable to those sampled in situ to avoid extrapolation beyond the model's reliable range. Finally, we repeated the joint-versus-single-model comparison using a larger, spatially independent regional replication dataset from the Saurashtra and Gulf of Kachchh coasts to assess whether the observed patterns were maintained beyond the original localised dataset.

Specifically, we tested three hypotheses: (1) that, due to HMSC's capacity for joint species modelling and its ability to account for residual associations among algal groups and shared environmental responses, multiband HMSC models would predict broad algal group cover more accurately than single-group models; (2) that, for the same reasons, multiband HMSC models would outperform index-based approaches (normalized difference vegetation index (NDVI), normalized difference water index (NDWI)); and (3) that spectral responses would differ among the major algal groups (green, red, and brown), reflecting their distinct pigment composition and structural characteristics.

Moreover, this study addresses an important research gap: although India has an extensive and ecologically diverse coastline, RS studies of intertidal habitats remain limited. Previous efforts have largely focused on specific fauna (e.g. molluscan diversity; Meyer et al. 2015; D'Souza et al. 2022) or broad vegetation types, with only a single study mapping the spatial extent of seaweed habitat (Bhavana et al. 2025) and a single earlier report partially mapping macroalgal groups (Nayak and Bahuguna 2001). This scarcity highlights an underexplored area of research and the potential of integrated approaches, such as the combination of RS and HMSC modelling, to advance our understanding of intertidal ecosystems.

## Materials and methods

### In situ sampling

The Gujarat coast forms the northwestern edge of the Indian peninsula and boasts India's longest coastline at 1617 km

(Geevan and Dixit 2012; Mahapatra et al. 2015; Beleem et al. 2019). The largely rocky-sandy habitat of the peninsula contains a range of tidal pools of varying sizes, intermittent mangroves, and smaller coral patches (Poriya et al. 2014).

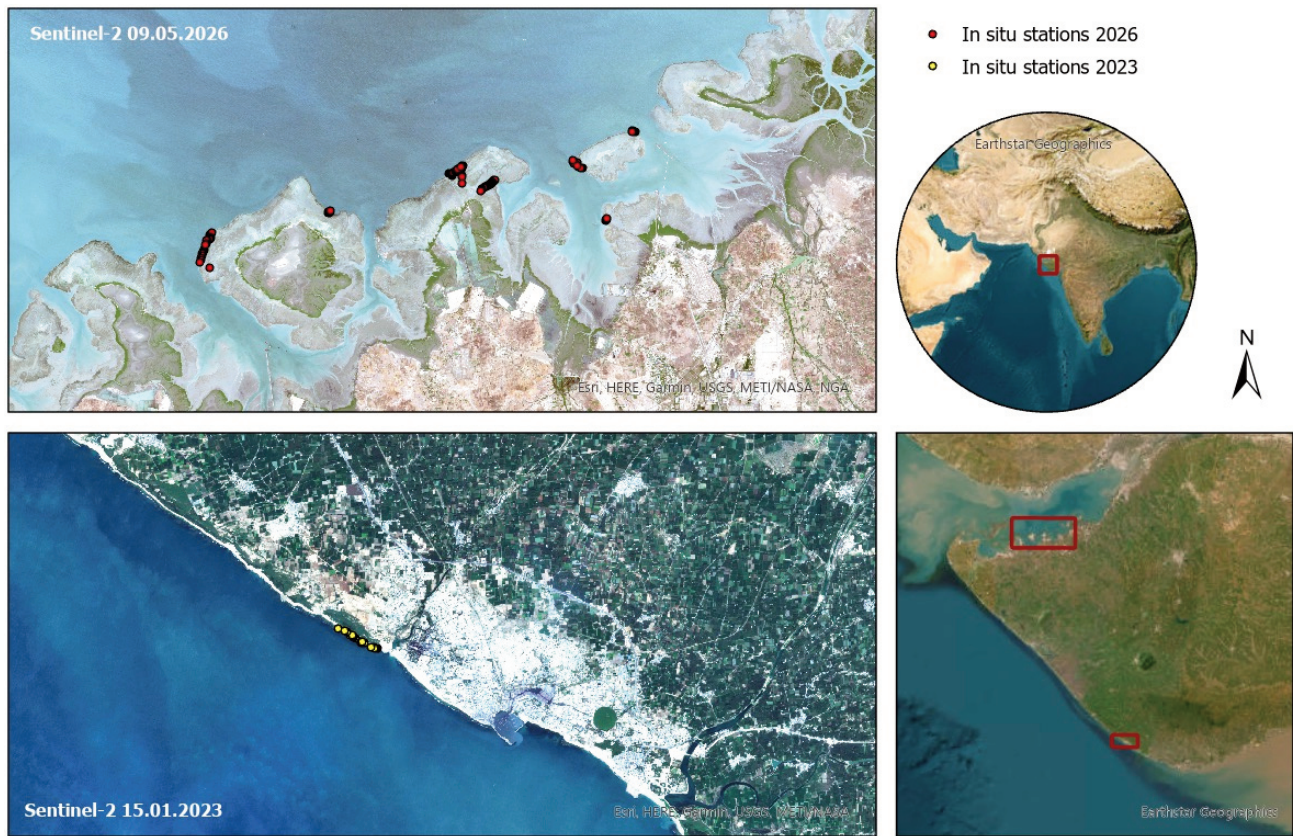
The first training dataset used in the present study was collected from the rocky intertidal zone of Veraval on the west coast of Gujarat, India. A second, independent dataset used to validate the modelling approach was collected from the broader Saurashtra and Gulf of Kachchh region (see below for details) (Fig. 1).

The Veraval coast features mixed semi-diurnal tides and a rocky intertidal zone with sandy patches, supporting diverse flora and fauna. This dynamic intertidal substratum extends horizontally and is interspersed with rock outcrops, crevices, extensive tidal pools, *Porites* coral colonies, and submerged zoanthid beds, and is home to diverse macrofaunal assemblages and seaweeds (Poriya 2015). With a tidal exposure between 600 and 850 m, the lower littoral zone ends in a steep descent towards the subtidal zone.

The seaweed diversity of the Veraval coast is vast, with 110 species documented (Jha et al. 2009). The intertidal zone is mainly dominated by red algae, with green algae thriving in water-filled pools, and rocky substrate often covered by brown and red algae. The diversity and extent of algal communities is largely seasonal, with optimum growth in winter. However, intertidal topography, exposure time, tidal amplitude, and grazing also affect algal cover.

The upper intertidal zone is dominated by the green alga *Ulva lactuca* (Chlorophyta), while *Platysiphonia* sp. (Rhodophyta) and a few brown algae are present only sparsely due to prolonged periods of emersion. The rock, which is largely barren, is covered mainly by the coralline alga *Peyssonnelia obscura* (Rhodophyta). The middle zone, with its abundance of waterlogged pools and puddles, supports a rich diversity of seaweed even in summer. *Sargassum* spp. (Phaeophyceae) and *Caulerpa racemosa* (Chlorophyta) thrive here, along with other species such as *Acrosiphonia orientalis* (Chlorophyta), *Gelidiella acerosa*, *Gracilaria corticata*, *Gelidium microp-terum*, and *Gelidium pusillum* (Rhodophyta). The edges of the exposed rock are covered mainly by *Amphiroa anceps* and *A. fragilissima* (Rhodophyta), and the sandy, calcified soft rock supports *Chondracanthus acicularis* (Rhodophyta). The lower littoral zone, which is subject to heavy spray, supports different seaweed communities than the upper and middle zones due to its minimal tidal exposure and submerged pools. Dense patches of *Sargassum* spp. and *Polycladia indica* (formerly *Cystoseira indica*) (Phaeophyceae) thrive here, with other seaweeds such as *Chamaedoris auriculata*, *Bryopsis plumosa*, *Codium dwarkense*, *Neomeris annulata* (Chlorophyta), and *Spatoglossum asperum* (Phaeophyceae) appearing patchily, along with a sparse presence of *Acetabularia calyculus* (Fig. 2).

Sampling was conducted on 11 and 12 January 2023, covering all predominant intertidal seaweed habitats identifiable through remote sensing methods (Kotta et al. 2014; Kutser et al. 2020). Most habitats remained exposed during the sampling period, except for those in the lowest intertidal zone, which were submerged to a maximum depth of 0.5 m.



**Fig. 1.** Study areas and in situ sampling stations along the Gujarat coast, India. The left panels show Sentinel-2 MSI Level-2A imagery acquired on 9 May 2026 for the Saurashtra and Gulf of Kachchh study region, and on 15 January 2023 for the Veraval study region. Red dots indicate stations sampled in 2026, and yellow dots indicate stations sampled in 2023. The red boxes in the overview maps on the right show the locations of the two study regions.



**Fig. 2.** Typical green (*Ulva lactuca*, *Caulerpa racemosa*), brown (*Spatoglossum asperum*), and red seaweed (*Gelidium micropterum*) habitats in the study area. Photos taken by the authors.

Sampling locations were selected using a stratified-random design to represent the principal intertidal habitats and a broad range of mixtures among green, brown, and red algae. A central GPS coordinate was recorded for each  $10 \times 10$  m field plot (Wu and Li 2009; Yu and Ma 2015). Each station represented a uniform habitat spanning  $100 \text{ m}^2$ , characterised either by a monospecific stand or a distinct mixture of multi-species assemblages. A preliminary visual inspection at this scale quantified total seaweed species coverage, followed by an assessment of individual species coverage. When field identification of species was challenging, small samples were collected for laboratory analysis. Green and red seaweeds

were predominant across the sampled sites, with brown seaweeds present at only one-third of the stations and consistently showing low coverage. Among the green seaweeds, *Ulva lactuca*, *Caulerpa racemosa*, and *Valoniopsis* sp. (Chlorophyta) were most prevalent, while *Porphyra* sp., *Gelidium micropterum*, and *Amphiroa* sp. (Rhodophyta) dominated among the red seaweeds. When brown seaweed coverage was higher in a patch, it predominantly consisted of *Spatoglossum asperum* and *Polycladia indica*.

Across sampling stations, green algal cover ranged 10–90% (mean 51%, SD 21), red algal cover 0–90% (mean 34%, SD 23), and brown algal cover 0–35% (mean 5%, SD 9).

Brown algae were present at 7 of 25 stations, consistent with their description as patchy and generally low in cover. Some stations were strongly dominated by a single algal group (e.g.  $\geq 70\%$  cover of green or red algae at 7 sites), whereas others comprised mixed assemblages where two groups contributed substantially to total cover.

To evaluate model transferability beyond the original Veraval dataset, we conducted additional field surveys in comparable intertidal habitats along the Saurashtra and Gulf of Kachchh coasts of Gujarat between 6 and 21 May 2026, thereby generating a spatially independent regional replication dataset (Fig. 1). The external dataset comprised 132 geo-referenced  $10 \times 10$  m sampling units. Percentage cover was estimated separately for green, brown, and red seaweeds at each sampling unit. Across the samples, green algal cover ranged 0–40% (mean 16%, SD 11), brown algal cover 0–65% (mean 36%, SD 16), and red algal cover 0–40% (mean 8%, SD 7), while total seaweed cover ranged 4–100% (mean 60%, SD 23). Green algae were present at 131 of 132 stations, brown algae at 126 of 132 stations, and red algae at 124 of 132 stations, indicating broad cover gradients and frequent co-occurrence among groups. Most stations represented mixed assemblages: all three algal groups co-occurred at 119 stations, and two groups each reached at least 20% cover at 64 stations. A smaller subset was dominated by a single algal group, with one group contributing at least 70% of the total seaweed cover at 11 stations. Among the green seaweeds, *Ulva lactuca* and *Ulva* sp. were the most frequently recorded taxa, often occurring together with *Caulerpa racemosa*, *C. taxifolia*, *C. sertularioides*, *Halimeda tuna*, and *Acrosiphonia orientalis*. Brown seaweeds were mainly represented by *Sargassum tenerrimum*, *Sargassum swartzii*, *Padina gymnospora* and *P. tetrastromatica*, and *Stoechospermum polypodioides*; occasional records also included *Lobophora variegata*, *Dictyopteris acrostichoides*, and *Spatoglossum asperum*. Among the red seaweeds, coral-line algae were most frequently observed, together with *Gracilaria corticata* and *G. dura*, and *Amphiroa anceps* and *Hypnea* sp.

### Remote sensing data acquisition and processing

This study acquired RS data from the European Space Agency's (ESA) S2 satellite. S2 is a freely available multi-spectral sensor with medium spatial resolution (up to 10 m) and short temporal revisit time (5 days at the equator). Table 1 presents the central wavelengths of the S2 spectral bands along with their respective spatial resolutions.

Several cloud-free S2 scenes were available around the Veraval field campaign, including images acquired on 5, 10, 15, and 20 January 2023. The scene acquired on 15 January 2023 was selected following a visual quality assessment because the study area was cloud-free, no substantial sun glint was visible, water clarity was highest, seabed features were clearly visible in shallow water, and the sampled intertidal habitats were exposed or nearly emerged at acquisition. This scene also closely matched the in situ survey conducted on 11–12 January 2023.

**Table 1.** Central wavelengths and native spatial resolutions of the Sentinel-2 spectral bands. The HMSC models used B2, B3, B4, B5, B6, B7, B8, B8a, and B9 as predictors

| Band | Central wavelength (nm) | Spatial resolution (m) |
|------|-------------------------|------------------------|
| B1   | 443                     | 60                     |
| B2   | 490                     | 10                     |
| B3   | 560                     | 10                     |
| B4   | 665                     | 10                     |
| B5   | 705                     | 20                     |
| B6   | 740                     | 20                     |
| B7   | 783                     | 20                     |
| B8   | 842                     | 10                     |
| B8a  | 865                     | 20                     |
| B9   | 945                     | 60                     |
| B10  | 1375                    | 60                     |
| B11  | 1610                    | 20                     |
| B12  | 2190                    | 20                     |

In contrast, substantially fewer high-quality S2 images were available for the Saurashtra and Gulf of Kachchh study region in May 2026. Cloud cover was more frequent than in January 2023, considerably reducing the number of usable scenes. Water transparency was also lower, likely due to pre-monsoon conditions, including stronger wind-driven sediment resuspension and increased biological activity. Following the visual quality assessment, the S2 image acquired on 9 May 2026 was selected because it offered the best overall combination of cloud-free conditions and underwater visibility.

S2 Level-2A bottom-of-atmosphere (BOA) reflectance data were downloaded from the Copernicus Data Space Ecosystem. The spectral layers were resampled to a common 10 m grid and cropped to the Veraval study area using the Sentinel Application Platform (SNAP). Standard Sen2Cor Level-2A processing is not optimised specifically for aquatic remote sensing. Its use was considered appropriate here because the analysis was restricted to exposed or nearly emerged intertidal habitats, but the resulting relationships should not be assumed to transfer directly to submerged vegetation. No additional adjacency-effect correction was applied beyond the standard Level-2A processing.

The optically deep water (ODW) mask was designed to distinguish optically shallow water, where bottom reflectance contributes to the satellite signal, from optically deep water, where the bottom signal is no longer detectable. This boundary was not defined using a fixed bathymetric threshold because optical penetration varies with water clarity. Spectral thresholds and indices were tested but did not provide reliable separation in the study area. We therefore applied a supervised minimum distance (MD) classification directly to the S2 reflectance data in ENVI geospatial analysis software, using training regions selected through visual interpretation. Several classification approaches were evaluated, and the MD result produced the most spatially consistent and visually realistic boundary. Because no independent reference dataset was available for the optically shallow–deep water boundary, a formal quantitative accuracy assessment was not possible;

the ODW mask was evaluated visually against the satellite imagery, and this limitation should be considered when interpreting the mapped predictions.

The central GPS coordinate of each  $10 \times 10$  m in situ field plot was linked to the corresponding cell in the common re-sampled 10 m S2 grid. No averaging across neighbouring cells or additional spatial interpolation was applied, and the field plots were not explicitly rotated or aligned with the satellite grid. Bands B2, B3, B4, and B8 have a native spatial resolution of 10 m; B5, B6, B7, and B8a have a native resolution of 20 m; and B9 has a native resolution of 60 m. Resampling aligned all bands to a common grid but did not increase their inherent spatial resolution. Geolocation uncertainty, boundary mixing, and the mismatch between the field-plot dimensions and the spatial support of the coarser bands are therefore acknowledged as sources of uncertainty.

Seaweed detection by RS is often hindered by the water column (Kutser et al. 2003; Klemas 2013), but the low-tide acquisition reduced rather than entirely eliminated such interference because the lowest intertidal stations could retain a very shallow water layer. Applications beneath a water column would require aquatic-specific atmospheric correction and explicit treatment of bathymetry, turbidity, and wavelength-dependent water-column attenuation. The green region of the spectrum is considered most suitable for detecting submerged aquatic vegetation (SAV) properties, particularly in turbid coastal waters (Kutser et al. 2003; O'Neill et al. 2011; Vahtmäe et al. 2020), whereas the near infrared (NIR) spectral region is considered the least usable because the vegetation signal decreases rapidly in the NIR region with increasing water depth (Kirk 1994). This renders NIR bands ineffective in underwater environments; however, some information can be obtained from the NIR region when the water column is very thin (less than  $\sim 1$  m) (Kutser et al. 2003).

Similarly, for the Saurashtra and Gulf of Kachchh coastal dataset, the field observations were linked to S2 Level-2A BOA reflectance values derived from low-tide, cloud-free imagery acquired on 9 May 2026 and processed using the same workflow as for the Veraval dataset. The same central-coordinate field-to-grid matching procedure was applied, without averaging neighbouring output cells; the native-resolution limitations of the coarser bands therefore also apply to this dataset.

### HMSC framework

We used HMSC through the R package *Hmsc* (Tikhonov et al. 2020) to investigate the relationships between remote sensing signals and the coverage of seaweed species groups, including green, brown, and red algae. When modelling the cover of various seaweed groups, we used nine S2 visible–near infrared (VIS–NIR) bands: B2, B3, B4, B5, B6, B7, B8, B8a, and B9 (Table 1), as these provide the most information on benthic vegetation when exposed. We retained all nine VIS–NIR bands, rather than pre-selecting a smaller subset or reducing dimensionality, for two reasons. First, we did not have conclusive *a priori* knowledge of which bands would best capture the cover of broad seaweed groups because the satellite reflectance of intertidal algal assemblages is influenced

not only by pigment absorption but also by canopy structure, morphology, hydration state, substratum, residual water films, and mixed-pixel effects. Second, although dimensionality reduction, for example through principal component analysis (PCA), can reduce the number of predictors, it transforms the original S2 bands into composite axes that are less directly interpretable.

The HMSC framework enabled the simultaneous modelling of multiple species groups, accounting for their co-occurrence patterns and dependencies on environmental covariates derived from RS. The modelling was performed using the package's default settings. We fitted HMSC models to untransformed percentage cover of green, brown, and red algae using a normal likelihood. The fixed-effect formula included nine additive linear S2 BOA reflectance covariates: B2, B3, B4, B5, B6, B7, B8, B8a, and B9. Since the relationships between reflectance and seaweed group coverage were nearly linear, the models were limited to linear terms. The joint model fitted the three algal groups simultaneously, whereas three otherwise equivalent single-group models were fitted separately for green, brown, and red algae.

Spatial structure was represented by a sample-level Gaussian predictive-process random effect, and the predictive-process random level was constructed with  $nKnots = 20$  from the projected sampling locations. Posterior sampling used four Markov chain Monte Carlo (MCMC) runs, a transient of 1000 iterations, a thinning interval of 10, and 500 retained posterior samples per chain, yielding 2000 retained posterior samples across chains. `GammaEta` was set to `FALSE`, and the remaining *Hmsc* priors retained their defaults. The joint and single-group models used the same response distribution, predictor set, spatial structure, MCMC settings, and cross-validation design. This within-framework comparison therefore evaluates the predictive value of estimating residual associations among algal groups while avoiding confounding with a different model family. Residual associations may also reflect unmeasured environmental variation and were not interpreted as evidence of causal biotic interactions.

Model performance was assessed using 5-fold cross-validation, where the data were split into five equal subsets. In each iteration, four folds (80% of the data) were used to train the model, and the remaining fold (20%) was used for validation. This process was repeated five times, with each subset serving once as the validation set. This approach quantifies predictive performance on unseen data rather than goodness of fit to the training data. Cross-validation (CV) statistics, including  $R^2$  and root-mean-square error (RMSE), were calculated using the `evaluateModelFit` function in the *Hmsc* package. We also fitted joint and single-group HMSC models to the enlarged validation dataset using the same predictors, model settings, and performance metrics as in the original analysis. This allowed us to assess whether the relative performance of joint versus single-group HMSC models was maintained when the approach was tested with substantially more observations from independent intertidal regions.

The `predict` function was employed to generate predictions across environmental gradients, while spatial predic-

tions were used to create maps illustrating the distribution of species groups. Care was taken to ensure the validity of these predictions, with particular emphasis on verifying that the extrapolated maps corresponded to intertidal seaweed habitats of a similar nature to the in situ training dataset. For the Veraval maps, posterior expected cover was calculated for each prediction cell from the fitted joint model and processed S2 predictor layers, averaged across posterior samples, and truncated at zero when the normal response model produced negative values before raster generation.

For the index-based comparison, we fitted two additional sets of HMSC models in which the individual S2 band predictors were replaced by a single spectral index, either the NDVI or the NDWI. Thus, NDVI and NDWI were evaluated in independent HMSC models, not as additional predictors in the multiband HMSC model. This comparison allowed us to evaluate whether models based on full spectral-band information explained seaweed group cover more effectively than HMSC models based on commonly used vegetation or water indices:

$$NDVI = \frac{B8 - B4}{B8 + B4}, \quad (1)$$

$$NDWI = \frac{B3 - B8}{B3 + B8}. \quad (2)$$

NDVI (Rouse et al. 1974) uses NIR (Band 8) and red (Band 4) reflectance, while NDWI (McFeeters 1996) uses green (Band 3) and NIR (Band 8) bands. Functionally, NDVI is designed to assess terrestrial vegetation health and density, while NDWI is better suited for water-rich environments, helping distinguish between water and vegetated areas. Both indices were calculated using the same training dataset as the HMSC model to assess their effectiveness in capturing seaweed group cover. Each single-index HMSC model used the same normal response distribution, spatial random-effect structure, MCMC settings, and five-fold cross-validation procedure as the multiband HMSC models, with the multiband fixed-effect formula replaced by either NDVI or NDWI as the sole predictor.

## Results

For the Veraval dataset, the HMSC models using B2, B3, B4, B5, B6, B7, B8, B8a, and B9 predicted green and red algal cover more accurately than brown algal cover. The joint model achieved  $CV R^2 = 0.61$  and  $CV RMSE = 13.1$  for green algae and  $CV R^2 = 0.55$  and  $CV RMSE = 15.4$  for red algae. The corresponding single-group models achieved  $CV R^2 = 0.52$  and  $CV RMSE = 15.3$  for green algae and  $CV R^2 = 0.61$  and  $CV RMSE = 14.5$  for red algae. Brown algal predictions were poor in both model structures (joint:  $CV R^2 = -0.06$ ,  $CV RMSE = 9.2$ ; single-group:  $CV R^2 = -0.09$ ,  $CV RMSE = 9.6$ ; Table 2).

The single-index HMSC models showed lower cross-validated predictive performance than the multiband HMSC models. The NDVI-based models achieved  $CV R^2 = 0.36$  for green algae ( $CV RMSE = 16.8$ ) and  $CV R^2 = 0.21$  for red

**Table 2.** Cross-validated predictive performance of the HMSC models for the Veraval coastal dataset.  $CV R^2$  and  $CV RMSE$  denote the coefficient of determination and root-mean-square error, respectively, calculated from predictions for held-out observations. Negative  $CV R^2$  values indicate that the model predicted the held-out observations less accurately than their mean response. RMSE is expressed in percentage-cover units. Here,  $n$  denotes the number of complete sampling units used to fit each model

| Seaweed group | Model       | $n$ | $CV R^2$ | $CV RMSE$ |
|---------------|-------------|-----|----------|-----------|
| Green         | Joint HMSC  | 25  | 0.61     | 13.1      |
| Green         | Single HMSC | 25  | 0.52     | 15.3      |
| Brown         | Joint HMSC  | 25  | -0.06    | 9.2       |
| Brown         | Single HMSC | 25  | -0.09    | 9.6       |
| Red           | Joint HMSC  | 25  | 0.55     | 15.4      |
| Red           | Single HMSC | 25  | 0.61     | 14.5      |

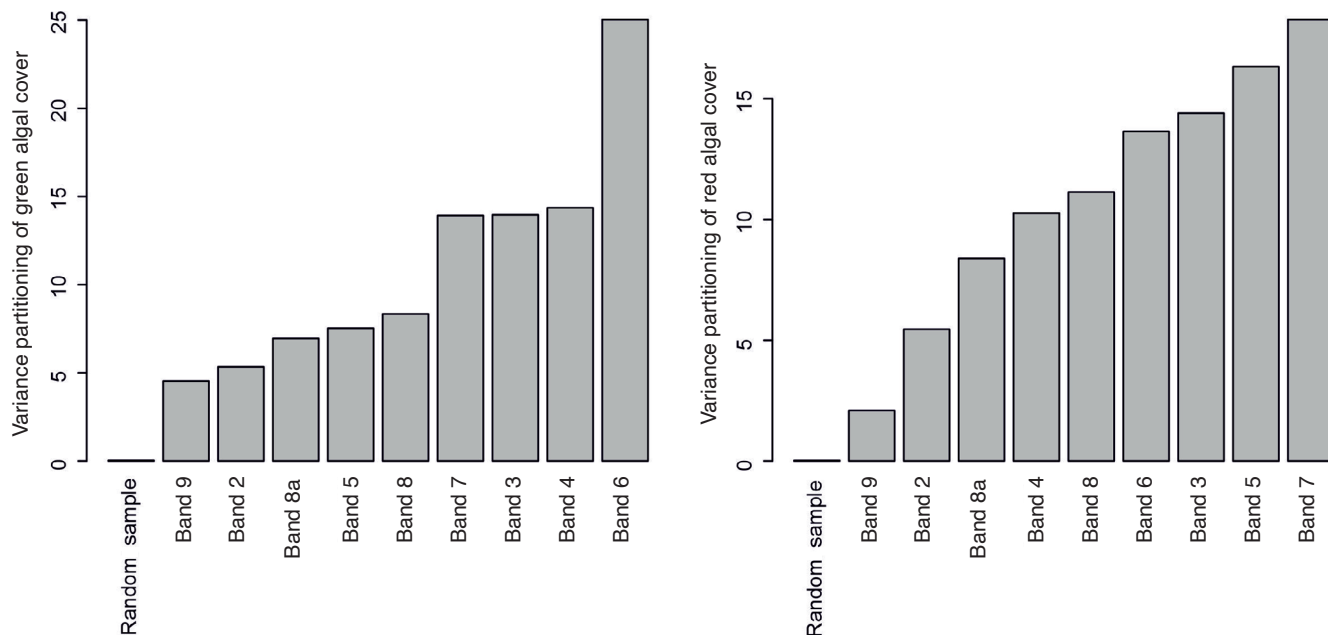
algae ( $CV RMSE = 20.4$ ). The NDWI-based model yielded  $CV R^2 = 0.34$  and  $CV RMSE = 17.0$  for green algae, whereas predictive performance was negligible for brown and red algae. Across the index-based models, brown algal predictions remained weak.

In the joint model, where B2, B3, B4, B5, B6, B7, B8, B8a, and B9 were used as predictors and all seaweed groups as dependent variables, multiple spectral bands contributed to explaining variation in their cover. Green and red seaweeds showed strong associations with B3–B9, with the strongest response in Band 6 for green algae and Bands 5 and 7 for red algae (Fig. 3). In the single-species models, similar bands were important, but the highest contribution shifted: Band 4 performed best for green algae, while Band 2 was most influential for red algae. Both joint and single models revealed linear relationships between green and red seaweed cover and reflectance bands. Green seaweed cover was negatively associated with reflectance in B2–B9, including B8a, while red seaweed cover showed a positive relationship with these bands (Figs 4–5).

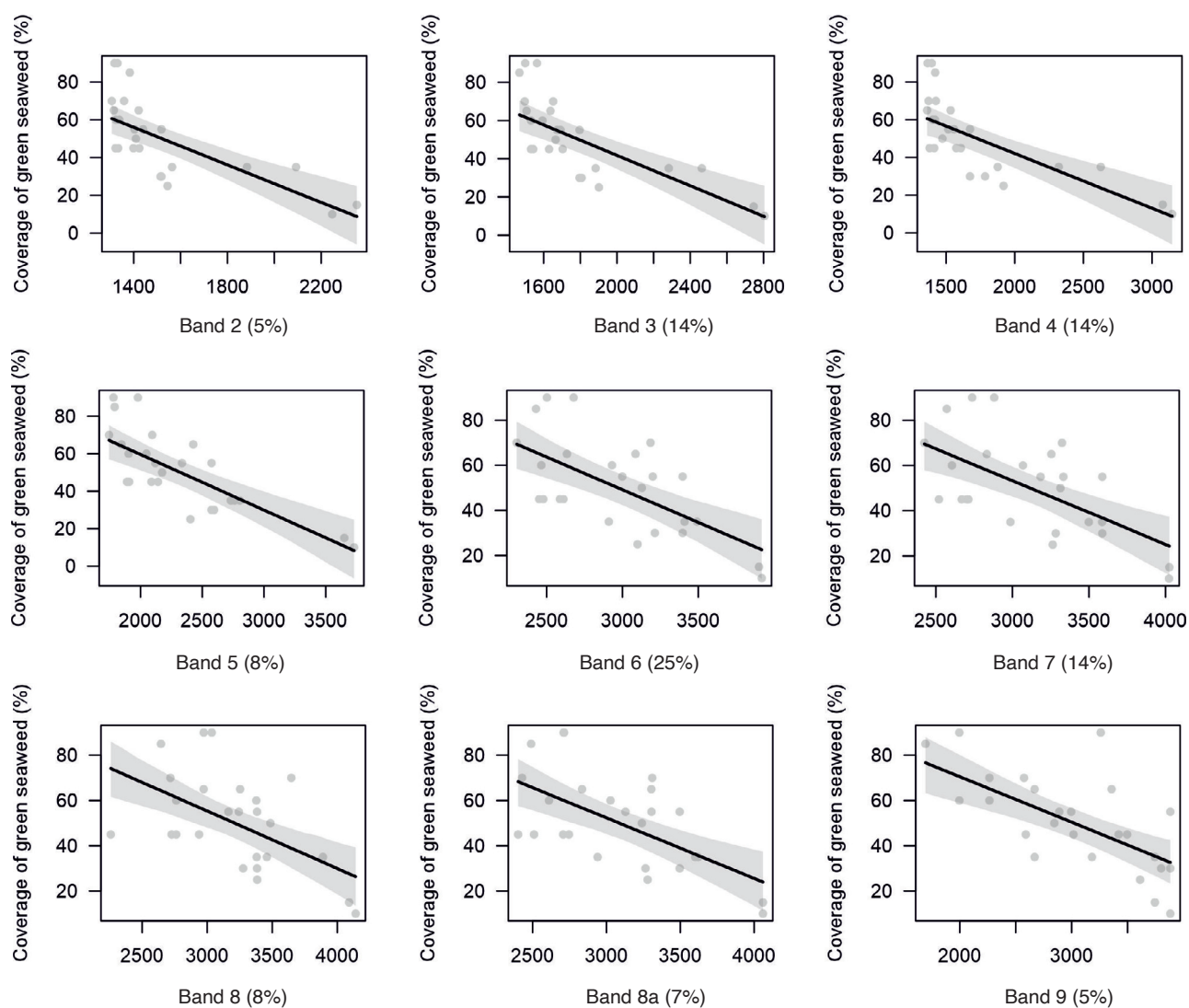
In the independent HMSC models using NDVI and NDWI as predictors of seaweed group cover, higher NDVI values were associated with increased green and decreased red seaweed cover, whereas NDWI showed the opposite pattern (Fig. 6). However, these relationships exhibited much greater variability compared to models based on individual spectral bands.

The joint HMSC model predicted widespread distribution of green and red algae along the Veraval coast. Green algae showed consistently high cover across most of the area, while red algae were generally less abundant. However, distinct high-cover hotspots for red algae were identified, particularly around the Veraval and Sutrapada towns (Fig. 7).

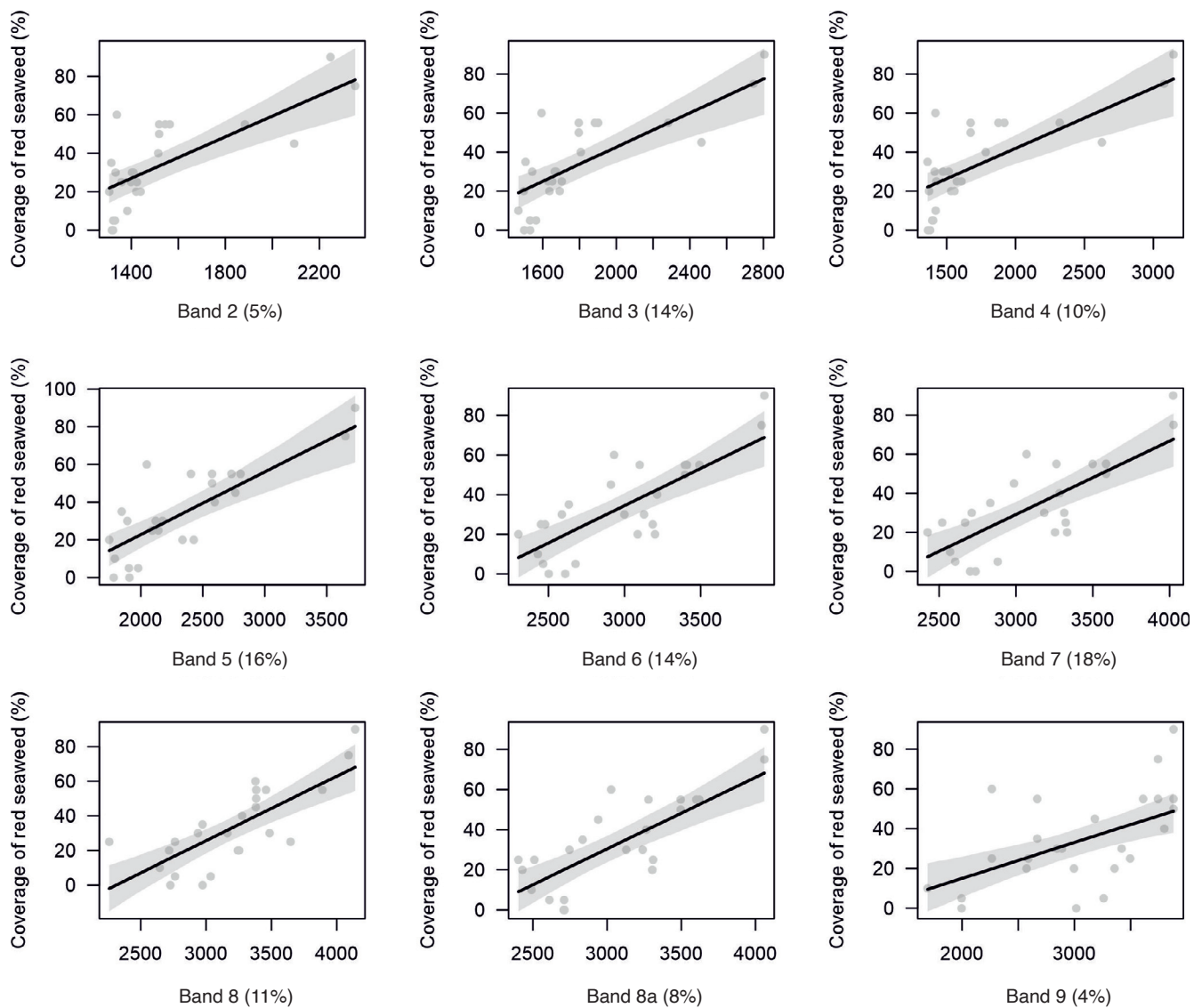
The independent regional replication analysis using data from the Saurashtra and Gulf of Kachchh coasts reproduced the principal performance pattern observed at Veraval: green and red algae were predicted more accurately than brown algae. In the replication dataset, the joint HMSC models consistently outperformed the corresponding single-group models. Joint and single-group  $CV R^2$  values were 0.798 and 0.773 for green algae, 0.225 and -0.386 for brown algae, and 0.701 and 0.616 for red algae, respectively. The improvement



**Fig. 3.** HMSC variance partitioning among Sentinel-2 spectral bands for green and red algal cover along the Veraval coast. Bars show the percentage contribution assigned to each band for the indicated algal group. Central wavelengths and native spatial resolutions of the bands are provided in Table 1.



**Fig. 4.** Modelled relationship between green algal cover and scaled Sentinel-2 Level-2A bottom-of-atmosphere reflectance in each focal band for the Veraval coast. The black line and grey ribbon represent the posterior median and 95% credible interval, respectively. Non-focal bands were assigned their most likely values conditional on each focal-band value rather than being held constant. Percentages in the panel labels are HMSC variance-partitioning contributions; central wavelengths and native spatial resolutions are given in Table 1.



**Fig. 5.** Modelled relationship between red algal cover and scaled Sentinel-2 Level-2A bottom-of-atmosphere reflectance in each focal band for the Veraval coast. The black line and grey ribbon represent the posterior median and 95% credible interval, respectively. Non-focal bands were assigned their most likely values conditional on each focal-band value rather than being held constant. Percentages in the panel labels are HMSC variance-partitioning contributions; central wavelengths and native spatial resolutions are given in Table 1.

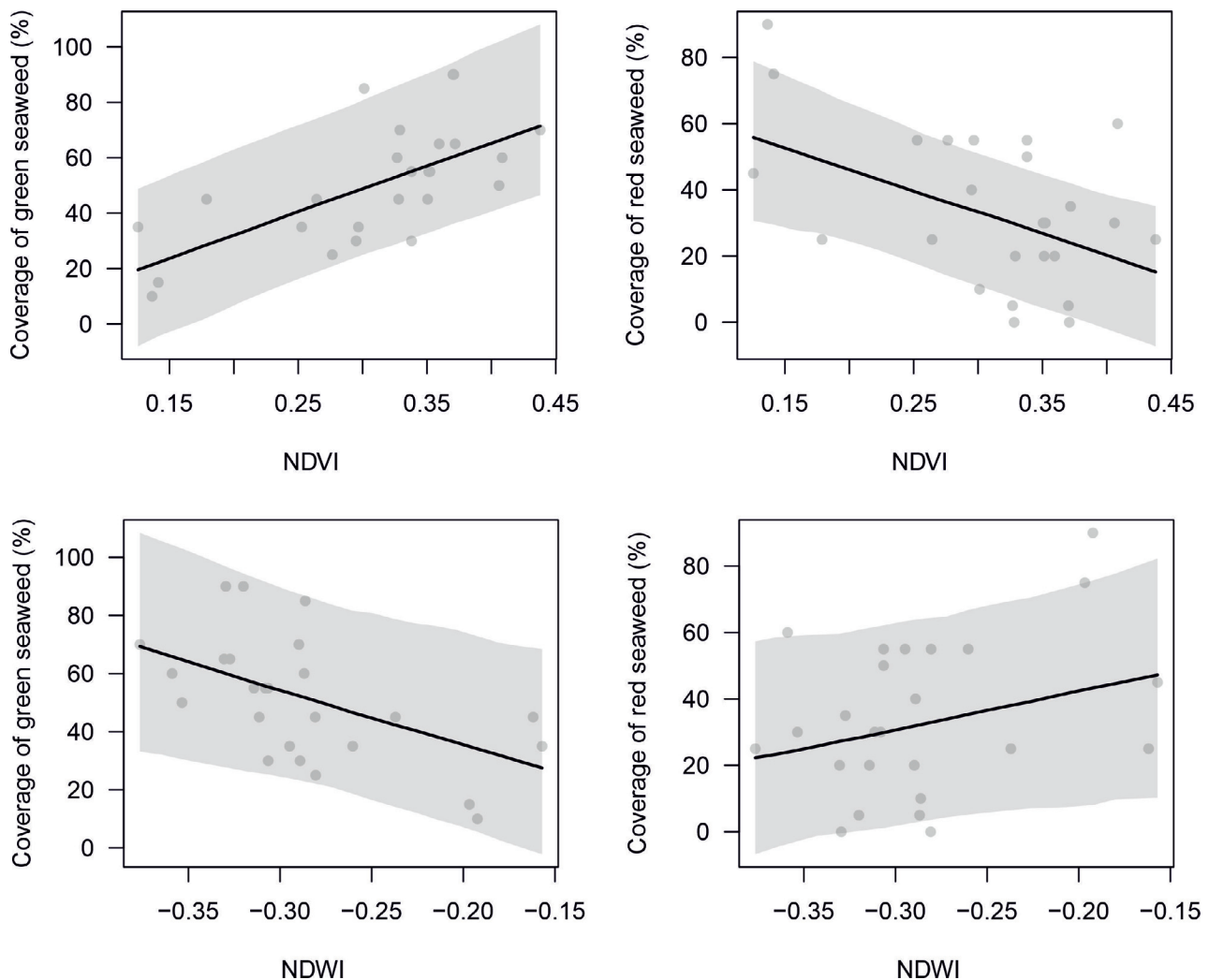
was greatest for brown algae, although its absolute predictive performance remained lower than that of green and red algae (Table 3; Figs 8–9).

## Discussion

Logistic challenges and time constraints are widely recognised when monitoring intertidal seaweed habitats. Although RS offers a promising alternative to traditional in situ methods, it is also subject to limitations, in particular in its ability to detect objects smaller than the spatial resolution of the sensor used. Therefore, the selection of an appropriate imaging technique is paramount to the effective monitoring of underwater habitats. Our research relied on S2 satellite imagery, an advantageous choice given its free availability, which promotes widespread application and facilitates the development and use of models to better understand biodiversity patterns. Given the previous successful use of this satellite to distinguish broader seaweed categories such as

green, brown, and red seaweed (Kotta et al. 2014), our strategy involved aggregating the taxonomic resolution of our in situ observations to these broad categories. This aggregation served to mitigate the potential for spurious noise propagation within our predictive models, thereby providing a tractable proof-of-concept approach to habitat analysis.

In complex habitats such as intertidal regions, the co-existence of multiple species or species groups creates a scenario where the observed reflectance represents the combined contribution of all species/groups within the area. When focusing on a single species or group, this overlap introduces significant noise into the model. This challenge highlights the need for a modelling algorithm capable of addressing such multivariate contexts. HMSC offers an effective solution: it is a multivariate statistical framework that integrates species occurrence or abundance data with environmental covariates, such as RS imagery. Its hierarchical properties enable simultaneous modelling of multiple species while accounting for their co-occurrence patterns and dependencies on RS signals



**Fig. 6.** Posterior relationships between NDVI or NDWI and green or red algal cover in the independent single-index HMSC models for the Veraval coast. Black lines show posterior median relationships and grey ribbons show 95% credible intervals. NDVI and NDWI formulas and their constituent Sentinel-2 bands are defined in the 'Materials and methods' section.

(Ovaskainen et al. 2017). To date, HMSC has primarily been applied to explore key questions in community ecology, with its potential applications in other fields yet to be fully realised.

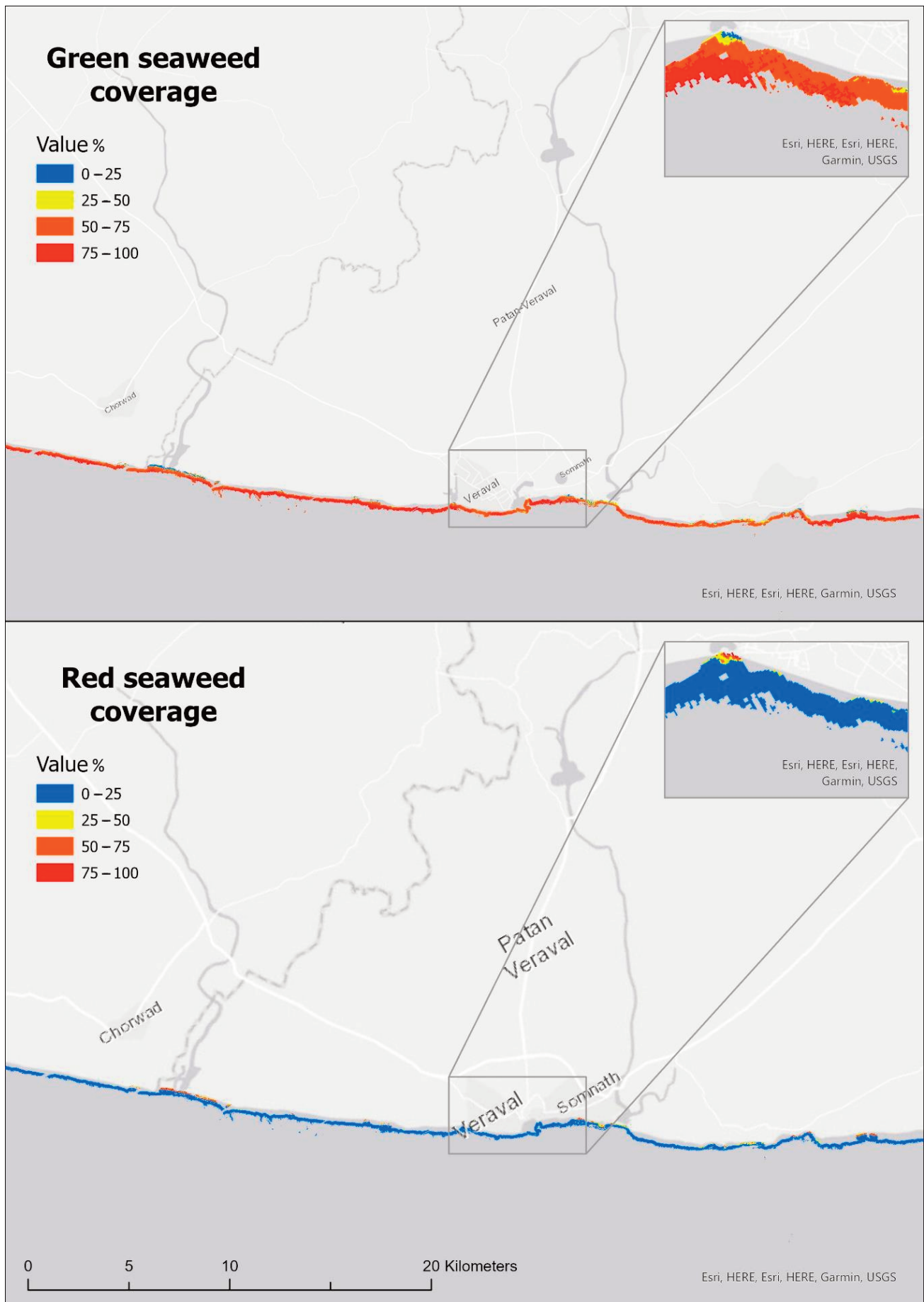
The multiband HMSC models showed higher cross-validated predictive performance than the single-index HMSC models based separately on NDVI or NDWI. This result supports the value of retaining information from the individual S2 bands.

For the Veraval dataset, the joint-versus-single comparison produced mixed results: the joint model performed better for green algae and slightly better for brown algae, although both brown algal models performed poorly, whereas the single-group model performed better for red algae. By contrast, in the spatially independent Saurashtra and Gulf of Kachchh regional replication dataset, the joint models consistently outperformed the corresponding single-group models for all three algal groups. This pattern supports a potential predictive benefit of modelling residual associations among algal groups.

Training-data scarcity plausibly contributed to the weak brown algal predictions at Veraval, where brown algae occurred at only 7 of 25 stations and averaged 5% cover. It cannot, however, explain their weaker relative performance in

the Saurashtra and Gulf of Kachchh dataset, where brown algae occurred at 126 of 132 stations, averaged 36% cover, and spanned a broad cover gradient. None of the joint-model coefficients for individual S2 bands had a 95% credible interval excluding zero, and approximately two-thirds of the variance-partitioning total was assigned to the spatial random effect. This indicates that brown algal cover was only weakly aligned with the linear spectral predictors used here. A likely contributing factor is that the brown algal category combined taxa with contrasting canopy forms and optical properties, including *Sargassum*, *Padina*, and *Stoechospermum*, within pixels that commonly also contained green and red algae and variable substrata. Such within-group optical heterogeneity and mixed-pixel effects, together with the limited spectral resolution of S2 and optical similarity among algal groups (Kutser et al. 2003), can obscure a group-specific reflectance signal even when brown algae are abundant. The joint model nevertheless provided modest positive predictive performance for brown algae, consistent with the joint multivariate structure providing predictive information not captured by the brown algal spectral response in the single-group analysis.

Multi-band models predict seaweed cover better than single-band or index-based models, even though indices also



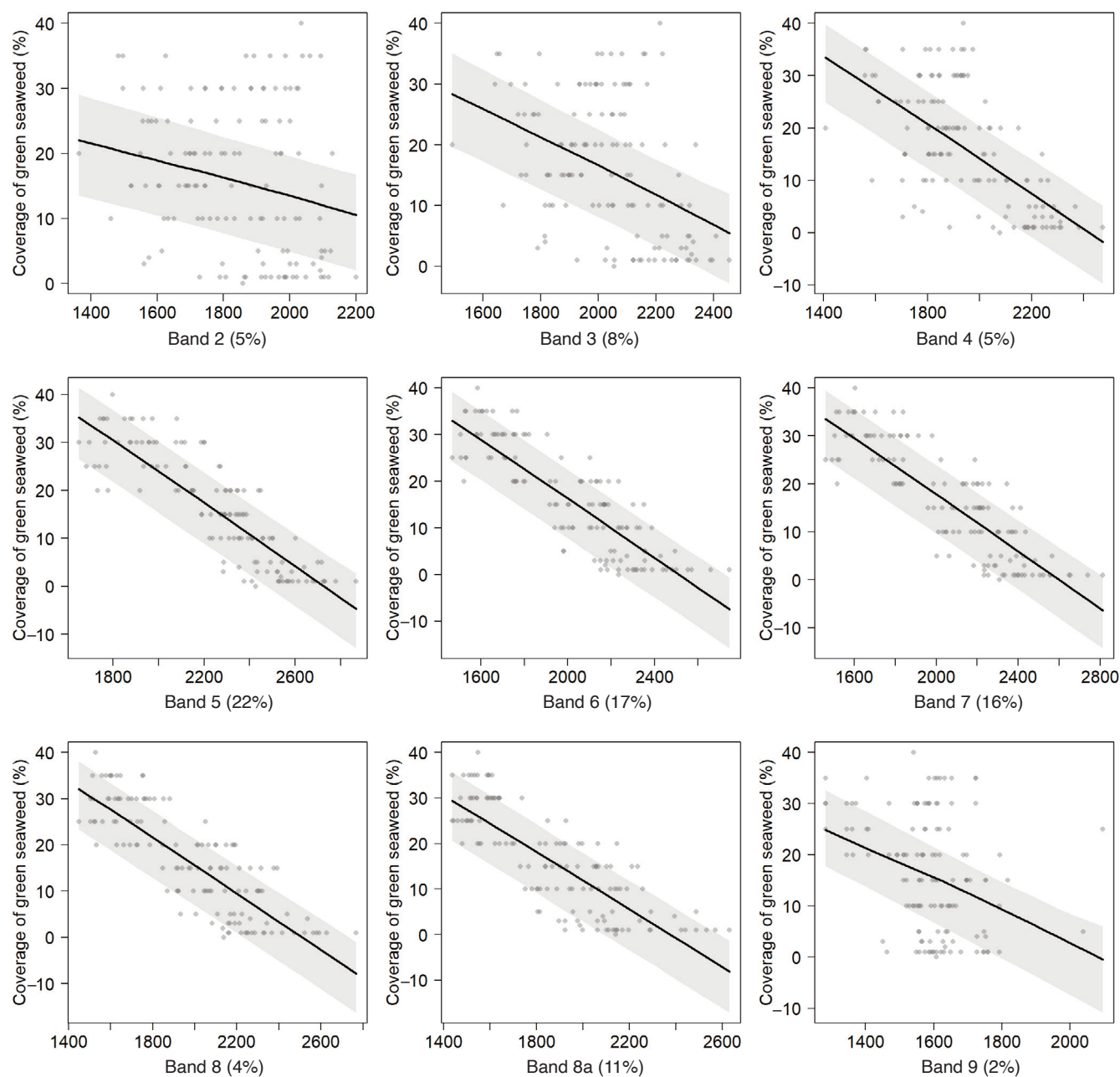
**Fig. 7.** Predicted green and red algal cover along the Veraval coast based on the joint HMSC model. Predictions were restricted to intertidal habitat patches comparable to the in situ training sites. The optically deep-water mask was derived from the supervised classification, and the land mask was based on the Gujarat coastline polygon. Enlarged panels are provided for both green and red algal cover to facilitate comparison of their nearshore distributions and the locations of red algal hotspots.

**Table 3.** Cross-validated predictive performance of the HMSC models for the Saurashtra and Gulf of Kachchh coastal dataset. CV  $R^2$  and CV RMSE denote the coefficient of determination and root-mean-square error, respectively, calculated from predictions for held-out observations. Negative CV  $R^2$  values indicate that the model predicted the held-out observations less accurately than their mean response. RMSE is expressed in percentage-cover units. Here,  $n$  denotes the number of complete sampling units used to fit each model

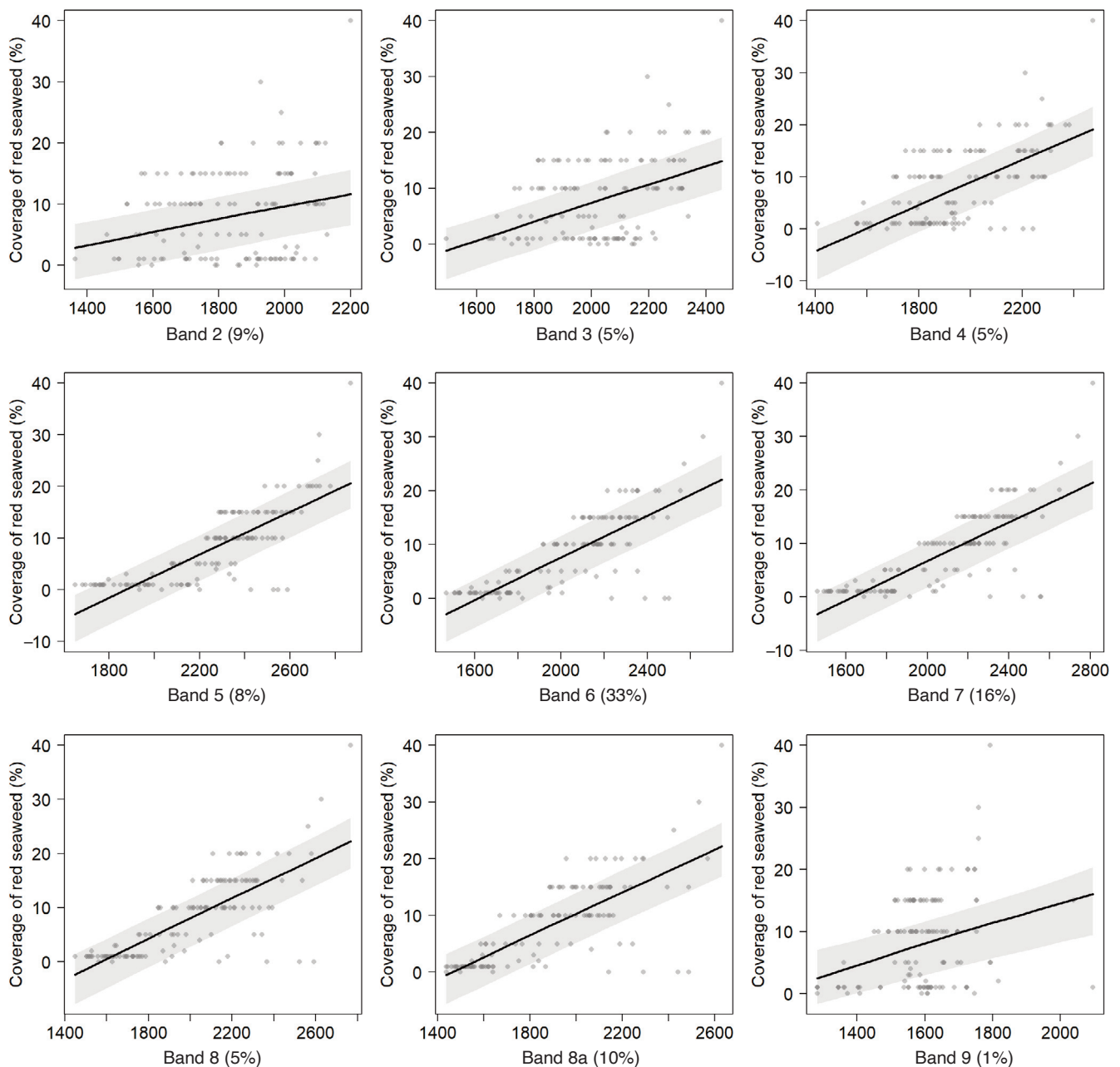
| Seaweed group | Model       | $n$ | CV $R^2$ | CV RMSE |
|---------------|-------------|-----|----------|---------|
| Green         | Joint HMSC  | 131 | 0.798    | 5.05    |
| Green         | Single HMSC | 132 | 0.773    | 5.33    |
| Brown         | Joint HMSC  | 131 | 0.225    | 14.31   |
| Brown         | Single HMSC | 132 | -0.386   | 19.06   |
| Red           | Joint HMSC  | 131 | 0.701    | 4.04    |
| Red           | Single HMSC | 131 | 0.616    | 4.58    |

use multiple bands. While reflectance-based indices have been used to map underwater vegetation (Cho et al. 2008; Cho et al. 2012; Villa et al. 2014), the inclusion of diverse bands enhances predictive performance, especially in complex, species-rich habitats (Cho et al. 2007; Féret and Asner 2014). This is because different species, due to their structural and chemical traits, occupy distinct spectral niches (Asner and Martin 2009). Relying solely on limited-band indices can therefore reduce model performance. This finding supports future research into combining multiple spectral bands to enhance model performance.

The HMSC model performed well despite limited training data, coarse resolution, and few spectral bands, demonstrating its robustness in linking RS signals to seaweed group cover, even in mixed communities. While the spatial predictions



**Fig. 8.** Modelled relationship between green algal cover and scaled Sentinel-2 Level-2A bottom-of-atmosphere reflectance in each focal band for the Saurashtra and Gulf of Kachchh coasts. The black line and grey ribbon represent the posterior median and 95% credible interval, respectively. Non-focal bands were assigned their most likely values conditional on each focal-band value rather than being held constant. Percentages in the panel labels are HMSC variance-partitioning contributions; central wavelengths and native spatial resolutions are given in Table 1.



**Fig. 9.** Modelled relationship between red algal cover and scaled Sentinel-2 Level-2A bottom-of-atmosphere reflectance in each focal band for the Saurashtra and Gulf of Kachchh coasts. The black line and grey ribbon represent the posterior median and 95% credible interval, respectively. Non-focal bands were assigned their most likely values conditional on each focal-band value rather than being held constant. Percentages in the panel labels are HMSC variance-partitioning contributions; central wavelengths and native spatial resolutions are given in Table 1.

illustrate the model's potential, they should be interpreted cautiously due to the small training dataset. Expanding the dataset, both spatially and across seasons, would likely improve reliability. Still, the study confirms the effectiveness of HMSC in capturing key seaweed–spectral relationships.

The predictive value of joint modelling depends not simply on observed co-occurrence but on whether the multivariate structure supplies information about one group after the measured spectral predictors and spatial structure are considered. The three algal groups frequently co-occurred in the Saurashtra and Gulf of Kachchh dataset, and the joint model produced better predictions than the corresponding single-group model for every group, with the largest difference for brown algae. This pattern indicates a predictive benefit from shared multivariate structure but should not be inter-

preted as evidence of causal biotic interactions. Specifically, when the model identifies strong relationships between different biotic elements, information derived from a robust RS signal for one element can be exploited to predict patterns of another element, even when the latter is not well captured by RS data.

Green algae contain chlorophyll a and b, as do vascular plants, including aquatic macrophytes, giving them a bright green appearance. They strongly absorb red light (Band 4) and reflect green (Band 3), which explains why the red band (Band 4) emerged as a key predictor in the single-group model. Areas with dense green algal cover appear darker in the red band due to chlorophyll absorption, distinguishing them from bare rock or sand. In contrast, the joint model aimed to detect spectral features that broadly explain variation across all

**Table 4.** Posterior band-level regression coefficients and variance-partitioning contributions from the joint HMSC model fitted to the Veraval coastal dataset. For each algal group and Sentinel-2 band,  $\beta$  is the posterior mean regression coefficient on the stored scaled bottom-of-atmosphere reflectance scale, posterior SD is the posterior standard deviation, and the 95% credible interval is bounded by the 2.5th and 97.5th posterior percentiles. Variance (Var.) contribution is the percentage of modelled variation assigned to the fixed-effect group by HMSC variance partitioning and is not a band-specific  $R^2$ ; the remaining percentage is assigned to the spatial random effect

| Group | Band | $\beta$ +/- SD     | 95% interval       | Var. contribution (%) | CV $R^2$ / RMSE |
|-------|------|--------------------|--------------------|-----------------------|-----------------|
| Green | B2   | -0.0083 +/- 0.0462 | [-0.0925, 0.1105]  | 5.3                   | 0.611 / 13.11   |
| Green | B3   | -0.0013 +/- 0.0346 | [-0.0625, 0.0640]  | 14                    | 0.611 / 13.11   |
| Green | B4   | -0.0170 +/- 0.0304 | [-0.0642, 0.0502]  | 14.4                  | 0.611 / 13.11   |
| Green | B5   | 0.0038 +/- 0.0182  | [-0.0297, 0.0432]  | 7.5                   | 0.611 / 13.11   |
| Green | B6   | -0.0234 +/- 0.0334 | [-0.0745, 0.0467]  | 25                    | 0.611 / 13.11   |
| Green | B7   | 0.0199 +/- 0.0359  | [-0.0384, 0.1038]  | 13.9                  | 0.611 / 13.11   |
| Green | B8   | 0.0168 +/- 0.0157  | [-0.0129, 0.0456]  | 8.3                   | 0.611 / 13.11   |
| Green | B8a  | -0.0168 +/- 0.0318 | [-0.0746, 0.0361]  | 6.9                   | 0.611 / 13.11   |
| Green | B9   | -0.0095 +/- 0.0048 | [-0.0187, -0.0001] | 4.5                   | 0.611 / 13.11   |
| Brown | B2   | -0.0009 +/- 0.0056 | [-0.0114, 0.0111]  | 8.4                   | -0.061 / 9.25   |
| Brown | B3   | 0.0001 +/- 0.0043  | [-0.0087, 0.0085]  | 12                    | -0.061 / 9.25   |
| Brown | B4   | -0.0009 +/- 0.0037 | [-0.0080, 0.0071]  | 11.8                  | -0.061 / 9.25   |
| Brown | B5   | 0.0013 +/- 0.0028  | [-0.0037, 0.0071]  | 12.2                  | -0.061 / 9.25   |
| Brown | B6   | -0.0011 +/- 0.0041 | [-0.0094, 0.0072]  | 14.2                  | -0.061 / 9.25   |
| Brown | B7   | 0.0023 +/- 0.0043  | [-0.0053, 0.0117]  | 14.4                  | -0.061 / 9.25   |
| Brown | B8   | 0.0012 +/- 0.0029  | [-0.0044, 0.0067]  | 10                    | -0.061 / 9.25   |
| Brown | B8a  | -0.0009 +/- 0.0038 | [-0.0088, 0.0061]  | 8.9                   | -0.061 / 9.25   |
| Brown | B9   | 0.0006 +/- 0.0016  | [-0.0025, 0.0038]  | 6.5                   | -0.061 / 9.25   |
| Red   | B2   | 0.0003 +/- 0.0295  | [-0.0505, 0.0689]  | 5.5                   | 0.555 / 15.42   |
| Red   | B3   | 0.0092 +/- 0.0228  | [-0.0315, 0.0559]  | 14.4                  | 0.555 / 15.42   |
| Red   | B4   | -0.0001 +/- 0.0209 | [-0.0350, 0.0459]  | 10.3                  | 0.555 / 15.42   |
| Red   | B5   | 0.0117 +/- 0.0128  | [-0.0121, 0.0391]  | 16.3                  | 0.555 / 15.42   |
| Red   | B6   | -0.0057 +/- 0.0225 | [-0.0446, 0.0413]  | 13.6                  | 0.555 / 15.42   |
| Red   | B7   | 0.0185 +/- 0.0243  | [-0.0245, 0.0731]  | 18.3                  | 0.555 / 15.42   |
| Red   | B8   | 0.0129 +/- 0.0118  | [-0.0114, 0.0347]  | 11.1                  | 0.555 / 15.42   |
| Red   | B8a  | -0.0054 +/- 0.0202 | [-0.0453, 0.0321]  | 8.4                   | 0.555 / 15.42   |
| Red   | B9   | 0.0013 +/- 0.0044  | [-0.0075, 0.0099]  | 2.1                   | 0.555 / 15.42   |

seaweed groups. This favoured bands indicating general vegetation presence. The prominence of red-edge (Bands 5–7) and NIR bands (Bands 8, 8a, and 9) in the joint model suggests that it captured general vegetation structure and biomass, as both green and red algae (when exposed) increase reflectance in these regions relative to bare substrate, driven more by structural than pigment-specific properties (e.g. Knipling 1970; Kutser et al. 2003; Vahtmäe and Kutser 2013).

Red seaweeds typically inhabit lower-shore or tidepool areas and may have had a water film over them during imaging, meaning they had not fully emerged. In such conditions, the blue band (Band 2) penetrates the water layer more effectively than red (Band 4) or NIR bands (Bands 8, 8a, and 9), explaining its importance in the single-group model. As with green seaweed in the joint model, the strong associations between red seaweeds and multiple bands likely reflect structural traits and canopy density rather than direct pigment absorption (Iriyama and Yoshiura 1977; Kirk 1994; Hedley and Mumby 2002; Chao Rodríguez et al. 2017; Saluri et al. 2019; Vahtmäe et al. 2025).

Algal morphology strongly influences spectral responses. Green algae such as *Ulva* have broad, flat blades that reflect light and may dry to a pale green-white colour, increasing infrared reflectance. In contrast, red algae such as *Gelidium* form dense, water-retaining turfs, while calcified forms such

as *Amphiroa* contain white calcium carbonate, which can enhance reflectance in several bands, including short-wave infrared (SWIR) bands (Bands 11–12) when dry. Although SWIR bands were not used as predictors in the HMSC models, these structural differences help illustrate why different algal groups can show distinct spectral cues across the Sentinel-2 bands used in the analysis. For example, *Ulva* may increase reflectance in the red-edge bands (Bands 5–6), whereas single-group models tend to rely on the band that best captures each group's dominant spectral trait, such as red-band absorption (Band 4) for green algae or blue-band response (Band 2) for red algae.

RS studies often predict a single object of interest using supervised classification, which involves learning an established classification from a training dataset. This dataset includes predictor variables measured for each sampling unit and assigns predefined classes to those units (Černá and Chytrý 2005). However, alternative approaches have been developed to model multiple objects simultaneously (see review by Kutser et al. 2020). For instance, artificial neural networks have been used to extract vegetation-type information in complex mapping problems; however, the underlying prediction process is opaque, reducing the interpretability of the results (Filippi and Jensen 2006). Similarly, fuzzy classification and decision tree approaches are useful in mixed-

**Table 5.** Posterior band-level regression coefficients and variance-partitioning contributions from the joint HMSC model fitted to the Saurashtra and Gulf of Kachchh coastal dataset. For each algal group and Sentinel-2 band,  $\beta$  is the posterior mean regression coefficient on the stored scaled bottom-of-atmosphere reflectance scale, posterior SD is the posterior standard deviation, and the 95% credible interval is bounded by the 2.5th and 97.5th posterior percentiles. Variance (Var.) contribution is the percentage of modelled variation assigned to the fixed-effect group by HMSC variance partitioning and is not a band-specific  $R^2$ ; the remaining percentage is assigned to the spatial random effect

| Group | Band | $\beta \pm$ SD       | 95% interval       | Var. contribution (%) | CV $R^2$ / RMSE |
|-------|------|----------------------|--------------------|-----------------------|-----------------|
| Green | B2   | -0.0059 $\pm$ 0.0111 | [-0.0284, 0.0152]  | 4.8                   | 0.798 / 5.05    |
| Green | B3   | -0.0082 $\pm$ 0.0118 | [-0.0319, 0.0152]  | 8.1                   | 0.798 / 5.05    |
| Green | B4   | 0.0065 $\pm$ 0.0091  | [-0.0105, 0.0251]  | 4.9                   | 0.798 / 5.05    |
| Green | B5   | -0.0150 $\pm$ 0.0068 | [-0.0294, -0.0023] | 21.6                  | 0.798 / 5.05    |
| Green | B6   | 0.0008 $\pm$ 0.0177  | [-0.0256, 0.0487]  | 17.1                  | 0.798 / 5.05    |
| Green | B7   | -0.0086 $\pm$ 0.0130 | [-0.0396, 0.0154]  | 16.4                  | 0.798 / 5.05    |
| Green | B8   | -0.0028 $\pm$ 0.0061 | [-0.0158, 0.0083]  | 4.4                   | 0.798 / 5.05    |
| Green | B8a  | -0.0082 $\pm$ 0.0093 | [-0.0268, 0.0099]  | 10.6                  | 0.798 / 5.05    |
| Green | B9   | -0.0066 $\pm$ 0.0067 | [-0.0178, 0.0071]  | 2.0                   | 0.798 / 5.05    |
| Brown | B2   | 0.0079 $\pm$ 0.0198  | [-0.0327, 0.0481]  | 2.5                   | 0.225 / 14.31   |
| Brown | B3   | -0.0044 $\pm$ 0.0216 | [-0.0498, 0.0347]  | 2.6                   | 0.225 / 14.31   |
| Brown | B4   | 0.0042 $\pm$ 0.0188  | [-0.0337, 0.0411]  | 2.1                   | 0.225 / 14.31   |
| Brown | B5   | -0.0050 $\pm$ 0.0136 | [-0.0341, 0.0172]  | 2.4                   | 0.225 / 14.31   |
| Brown | B6   | 0.0308 $\pm$ 0.0416  | [-0.0215, 0.1575]  | 9.5                   | 0.225 / 14.31   |
| Brown | B7   | -0.0018 $\pm$ 0.0286 | [-0.0766, 0.0460]  | 4.8                   | 0.225 / 14.31   |
| Brown | B8   | 0.0017 $\pm$ 0.0115  | [-0.0240, 0.0215]  | 1.8                   | 0.225 / 14.31   |
| Brown | B8a  | -0.0212 $\pm$ 0.0209 | [-0.0669, 0.0154]  | 6.1                   | 0.225 / 14.31   |
| Brown | B9   | 0.0070 $\pm$ 0.0190  | [-0.0196, 0.0421]  | 1.1                   | 0.225 / 14.31   |
| Red   | B2   | 0.0103 $\pm$ 0.0076  | [-0.0042, 0.0254]  | 9.5                   | 0.701 / 4.04    |
| Red   | B3   | 0.0033 $\pm$ 0.0077  | [-0.0127, 0.0176]  | 4.9                   | 0.701 / 4.04    |
| Red   | B4   | -0.0044 $\pm$ 0.0068 | [-0.0175, 0.0094]  | 4.9                   | 0.701 / 4.04    |
| Red   | B5   | 0.0047 $\pm$ 0.0046  | [-0.0046, 0.0131]  | 7.5                   | 0.701 / 4.04    |
| Red   | B6   | 0.0153 $\pm$ 0.0128  | [-0.0022, 0.0528]  | 33.1                  | 0.701 / 4.04    |
| Red   | B7   | 0.0046 $\pm$ 0.0088  | [-0.0184, 0.0197]  | 15.6                  | 0.701 / 4.04    |
| Red   | B8   | 0.0036 $\pm$ 0.0042  | [-0.0047, 0.0117]  | 5.3                   | 0.701 / 4.04    |
| Red   | B8a  | -0.0073 $\pm$ 0.0072 | [-0.0222, 0.0052]  | 9.6                   | 0.701 / 4.04    |
| Red   | B9   | 0.0003 $\pm$ 0.0046  | [-0.0080, 0.0090]  | 0.7                   | 0.701 / 4.04    |

class contexts, employing probability-based classifications rather than crisp classifications to determine class proportions within a pixel, thereby producing soft classifications (Xu et al. 2005). Although these methods yield multiple products simultaneously, the predictions for each object are made independently.

The spectral mixing model describes how materials in a scene interact to produce a composite spectrum within a pixel (Keshava et al. 2000). Spectral unmixing then deconstructs each mixed pixel into a collection of pure spectral signatures, or endmembers, along with their corresponding percentages or abundances. Bayesian methods are particularly effective in this context, as they can incorporate meaningful prior information into the modelling process, enabling robust statistical representation of variability and uncertainty in spectral data, abundances, and endmembers (Chen et al. 2017). However, the effectiveness of these methods often depends on the quality of the endmember spectrum library, which is frequently limited (Wei and Wang 2020). While this approach bears some resemblance to HMSC in methodology, the above techniques do not account for interactions among the objects of interest independently from how they are observed by the remote sensing sensor. When the goal is to detect biotic patterns, associations among biotic elements are a common phenomenon, and incorporating this knowledge can signifi-

cantly enhance the predictive performance of RS models.

The modelling approach presented in this study can be significantly enhanced by incorporating additional covariates (e.g. Kotta et al. 2013). While our low tide, emergent habitat design reduces the influence of the water column and thus the need to model depth and turbidity explicitly, applications to submerged or optically complex coastal waters would require the inclusion of water column variables such as bathymetry and turbidity. Importantly, the flexibility of the HMSC framework allows for the integration of multiple covariates. Commonly available resources for coastal areas worldwide are ocean physics- and biochemistry-modelled products. The spatial distribution of intertidal habitats is influenced by a complex interplay of environmental variables (Menge and Sutherland 1987; Kotta et al. 2017). Including these variables in a hybrid approach that combines RS with ocean modelling can substantially improve predictions. For instance, ocean models provide essential information on tidal regimes, wave intensity, salinity, nutrient availability, and other variables that influence species composition and the broader patterns of intertidal habitats, details that are often beyond the reach of RS instruments. Conversely, RS techniques excel at detecting microhabitat characteristics at specific sites, which cannot be predicted by ocean models alone. By integrating these complementary approaches, a more holistic perspective on inter-

tidal habitats can be achieved. Moreover, applying the models to several same-season images acquired under comparable tidal and atmospheric conditions would provide a valuable test of temporal robustness. Such an analysis should explicitly separate genuine temporal variability from differences caused by tidal stage, residual water films, illumination, and atmospheric conditions among scenes.

## Conclusion

This study demonstrates the potential of combining HMSC with S2 reflectance to predict green and red algal cover in exposed intertidal habitats. The independent regional replication confirmed the main group-specific performance pattern and consistently favoured the joint models, but it did not test direct geographical transfer of the fitted Veraval model. Brown algae remained less predictable even when well represented, highlighting limitations associated with spectral separability, mixed pixels, and within-group optical heterogeneity. Broader evaluation across seasons, coastlines, sensor types, and submerged conditions, together with direct comparison against machine-learning and spectral-unmixing approaches, is required before the generality of the method can be established.

## Data availability statement

The datasets used and/or analysed during the current study are available from the corresponding author at reasonable request.

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## Loodetevööndi suurvetikate leviku kaardistamine satelliidiandmete ja koosluste hierarhilise modelleerimise abil

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Loodetevööndi vetikakoosluste kaardistamist kaugseire abil raskendab samas satelliidipikslis esinevate vetikarühmade spektraalsete signaalide kattumine. Uuringus ühendasime Sentinel-2 satelliidiandmed koosluste hierarhilise modelleerimisega (HMSC), et hinnata rohe-, pruun- ja punavetikate levikut Indias Gujarati rannikul. Uurisime, kas teiste vetikarühmade kohta kogutud andmete kaasamine parandab iga rühma leviku ennustustäpsust. Analüüsisime esmalt Veravali ranniku andmeid ning kordasime analüüsi Saurashtra ranniku ja Kachchhi lahe ulatuslikuma andmestikuga. Ühismudel arvestas vetikarühmade koosesinemise mustreid ja nende seoseid spektraalsete tunnustega. Meetod võimaldas edukalt ennustada rohe- ja punavetikate levikut. Veravalis parandas vetikarühmade koos modelleerimine ennustustäpsust vaid osal rühmadest, ulatuslikuma piirkondliku andmestiku puhul aga kõigil kolmel rühmal. Tulemused näitavad, et vetikarühmade koosesinemist arvestavad mudelid võivad aidata satelliidiandmete põhjal täpsemalt kaardistada mõõna ajal veest välja jäävaid vetikakooslusi. Enne meetodi laiemat kasutamist tuleb selle ennustustäpsust kontrollida eri aastaagadel ja teistes rannikupiirkondades.