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An integrated approach to estimate aesthetic and ecological values of coralligenous reefs

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ABSTRACT

Assessing non-material nature contributions to people has become one major challenge in biodiversity sciences. Among them, the aesthetic value of biodiversity is of strong importance as it contributes to human well-being and increases the collective willingness to engage in conservation efforts. Using the endangered coralligenous reefs along the French Mediterranean coastline as a case study, we propose a quantitative approach to estimate the aesthetic and ecological values of a marine ecosystem. We combined human image evaluation and deep learning algorithms to provide a quantitative estimation of the aesthetic value of 7692 photographic quadrats among 160 stations located between 20 and 90 m depth and gathered on 95 sites. To understand how aesthetic value is related to biodiversity metrics, environmental variables and anthropogenic pressures we used a structural equation modelling approach. We found that taxonomic diversity and species composition explained a significant part of the aesthetic value of the coralligenous reefs. Taxonomic diversity showed a net positive effect and species composition analysis highlighted both positive and negative effects of some species on the aesthetic value. Net negative effects of functional and phylogenetic diversities were found, which illustrates an aesthetic bias in human perception of ecological value. The aesthetic and ecological values were mapped along the French Mediterranean coastline in three dimensions (longitude, latitude, depth); this synthetic visualization could be of strong interest for conservation and communication purposes about this endangered benthic key-ecosystem of the Mediterranean Sea. Overall, our approach provides a geographically scalable estimate of the aesthetic value of biodiversity which is still an underestimated facet of nature contributions to people. It could be transposed to other marine ecosystems such as coral reefs but also to terrestrial landscapes for which an increasing number of images evaluated for human preference are becoming available.

1. Introduction

Ecosystems are facing an unprecedented loss of species qualified as the sixth mass extinction of biodiversity (Steffen et al., 2015). Overexploitation, habitat destruction and climate change, led by human actions, are among the main drivers of this crisis with strong associated consequences on ecosystems' functioning and their contribution to humanity's welfare (IPBES, 2019). The IPBES (Intergovernmental science policy Platform on Biodiversity and Ecosystem Services) classified the Nature's Contributions to People (Díaz et al., 2018) into three categories: material (*e.g.* habitat creation, food and water supply), regulating (*e.g.* regulation of ocean acidification) and non-material (*e.g.* cultural benefits). While material and regulation services receive a lot of attention (de Groot et al., 2012; Small et al., 2017), the non-material

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services, such as Cultural Ecosystem Services (CES), are more difficult to evaluate and are only beginning to be assessed (Scholte et al., 2015; Small et al., 2017). Their evaluation requires new data and intensive methods at the intersection of social and biodiversity sciences (Steffen, 2009; Daniel et al., 2012; Mouchet et al., 2014; Tribot et al., 2018a, 2018b; Jarić et al., 2020).

CES relate to the positive impact of nature on people's state of mind (Díaz et al., 2018). This is exemplified by how conservation can be promoted through the emotional link humans have with nature (Cooper et al., 2016) due to the strong correlation between the human willingness to protect species or ecosystems and affective factors (*i.e.* emotional factors which influence human decision; Stokes, 2007; Martín-López et al., 2007). The cognitive response to the observation of the environment creates an aesthetic experience in the viewer's mind. Providing inspiration and contributing to well-being (MEA, 2005), nature aesthetic experience is thus one of the major CES (Shimamura and Palmer, 2011). It can be considered at different scales depending on the levels of human perception and ecological organization (Tribot et al., 2018a, 2018b). One of the simplest aesthetic experiences is the direct visual perception of species assemblages or individual species.

Species assemblages are particularly relevant to measure aesthetics as this ecological level of organization is used by ecologists to measure other metrics of biodiversity (Haas et al., 2015; Southon et al., 2017; Tribot et al., 2018a, 2018b, 2019; Fairchild et al., 2018). However, the few studies that directly measured the aesthetics of species assemblages often lack quantitative estimates of aesthetic value (Tribot et al., 2018a, 2018b) and thus cannot fully consider the interactions between aesthetic and ecological values. Most of these studies are based on expert knowledge or qualitative questionnaires (*e.g.*, Stokes, 2007; Beza, 2010) impeding generalization and reproducibility. Some other approaches, however, take advantage of increasing computational capacities to evaluate the human aesthetic preferences with a more scalable method. They analyze the mathematical information composing an image (Datta et al., 2006; Li and Chen, 2009; Haas et al., 2015) and extract features (*e.g.*, color distribution, luminance, saturation, fractal dimension) that are expected to discriminate between aesthetically pleasing and displeasing images (Haas et al., 2015). This approach opens new opportunities to study the aesthetic value of species assemblages while it still lacks a comparison between direct evaluation of human interest and indirect evaluation through computational analysis. Here we push this logic forward by taking advantage of a previous study where a quantitative estimate of the human preferences on coralligenous reefs was obtained through an online questionnaire (Tribot et al., 2016) from which we developed an intensive deep-learning algorithm which internally analyzes image features, to predict the aesthetic value of this ecosystem.

Coralligenous reefs (Fig. 1a) are among the richest ecosystems of the Mediterranean Sea (Bianchi and Morri, 2000; Ballesteros, 2006). They are found between 20 and 120 m deep and are composed of a biogenic substrate produced by encrusting algae and animal builders such as bryozoans and gorgonians (Learmonth et al., 2006). They host more

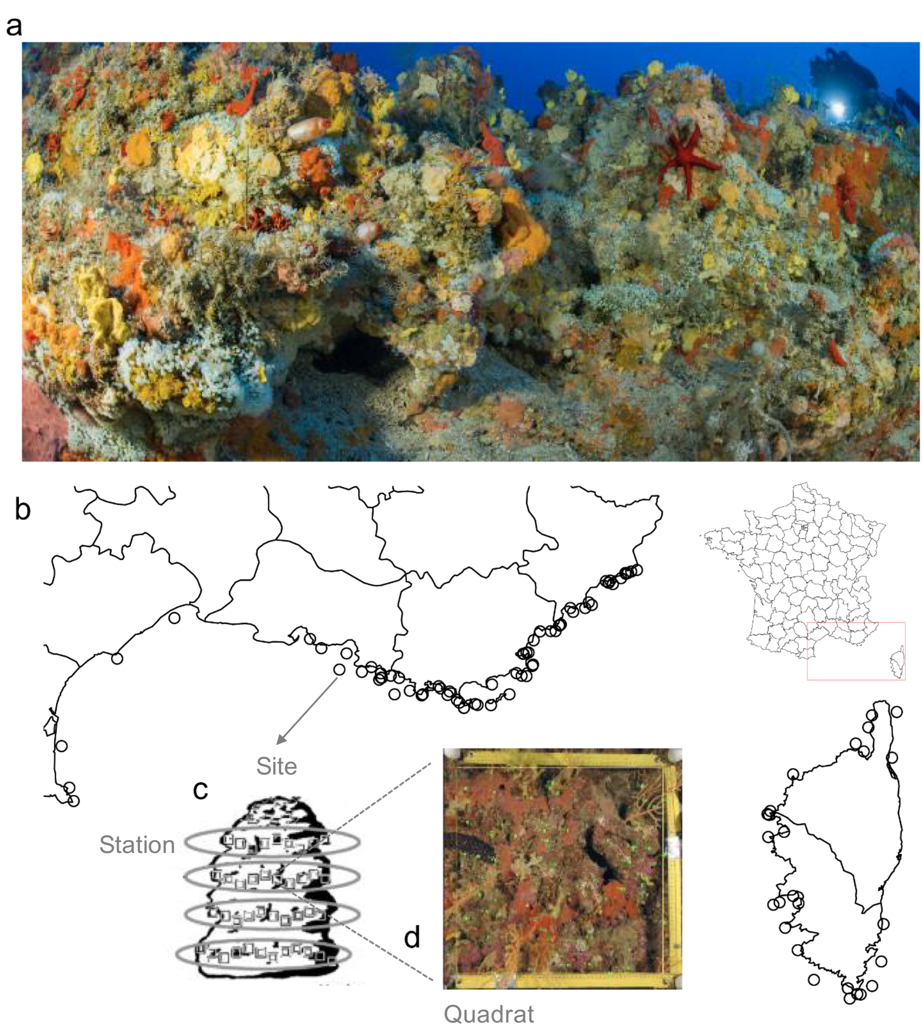

Fig. 1. Study area (a) Coralligenous reefs are biodiversity hotspots in the Mediterranean. They are biogenic substrates produced by encrusting algae, bryozoans and gorgonians and host more than 1700 species. They are found between 20 and 120 m deep, are considered as key marine ecosystems and are threatened by human activities. Photo © Laurent Ballesta from « Planete Méditerranée » book, 300p. Andromede Collection-Hemeria ed., www.laurentballesta.com. Photo taken by Laurent Ballesta (Copyright: Laurent Ballesta for Andromède Océanologie). Bottom: Map of the studied area. (b) Coralligenous reef sites along the French Mediterranean coastline are represented by grey dots. (c) For each site, one or several depths (stations) is/are studied and for each station, 30 photographic quadrats were taken. (d) 64 random points are identified on each photographic quadrat with the CPCe software. Adapted from Doxa et al. (2016).

than 1700 species and are, after the *Posidonia oceanica* meadows, the second benthic key-ecosystem of the Mediterranean Sea (Gili and Coma, 1998; Ballesteros, 2006; van der Heijden and Kamenos, 2015). Due to their structure and slow growth, coralligenous reefs are among the most vulnerable marine ecosystems (Ballesteros, 2006; Learmonth et al., 2006). The aesthetic value of coralligenous reefs was estimated in a previous study that took advantage of the Elo algorithm (Elo, 1978) to score 50 × 50 cm photographs, hereafter called quadrats of coralligenous reefs based on an online questionnaire presented to the public (Tribot et al., 2016). This method provided a quantitative and standardized measure of people's visual aesthetic preferences and showed that species richness, and to a lesser extent, functional richness, had a significant positive impact on the aesthetic value of coralligenous reefs. While important, these results were limited, as only a relatively small number of photographic quadrats could have been evaluated online (*e.g.*, more than 1000 participants were required to score 297 photographic quadrats). The coralligenous reefs survey used for this previous study contains thousands of photographic quadrats over 160 stations along the French Mediterranean coastline (RECOR survey, Deter et al., 2012a, 2012b) and thus there is a real opportunity in providing automatic evaluation of this large quantity of data.

Here we aim at (i) using a deep learning algorithm to predict the aesthetic values of the photographic quadrats from the RECOR survey database, (ii) combine these estimates with ecological metrics to see how they are related, and (iii) map the aesthetic value of coralligenous reefs along the French Mediterranean coastline. To achieve the second objective, the estimated aesthetic value has been compared to ecological values of these assemblages as well as to environmental variables and anthropogenic pressures. This allowed us to disentangle some of the drivers of the human aesthetic experience of this endangered ecosystem.

2. Material & methods

Most analyses were performed using R *v.3.6.0* (R Core Team 2020; specific functions within specific packages are indicated in italic). All relevant code and data are available from the associated GitHub repository (see Open research statement).

2.1. Photographic material

The RECOR survey was initiated in 2010 by Andromède Océanologie and the Rhône-Méditerranée-Corse water agency (https://medtrix.fr/). It is conducted along the French Mediterranean coastline on 160 stations located between 20 and 90 m depth gathered on 95 sites (Fig. 1b). To assess the composition of the coralligenous assemblages on each station, 30 photographic quadrats (50 × 50 cm) are randomly chosen over the monitored reef (Fig. 1c.). We used a total of 7692 photographic quadrats from 2010 to 2017. Due to the variation of sampling across the years for a site (Appendix A), the temporal dimension has not been taken into account. Thus, hereafter a station is composed of all the quadrats sampled at these latitude, longitude and depth disregarding the year in which they have been sampled. To supply the predictive model with images comparable to the learning data set, each photographic quadrat has been rescaled to 500 × 500 pixels and the variations of luminosity and color spectrum due to the use of different photographic material throughout the years of sampling have been corrected using a photoshop© color matching script.

2.2. Biodiversity data

On each photographic quadrat, 64 random points were selected using the CPCe 4.1 software « coralligenous assemblages' version » (Kohler and Gill, 2006; Deter et al., 2012a, 2012b, Fig. 1d.) and 177 benthic organisms have been identified at the species or genus level using nomenclatures by Appeltans et al. (2011), Guiry and Guiry (2013) and Rodriguez-Prieto et al. (2013). Based on these 64 points per quadrat, we computed the relative abundance of each of the 177 taxa. In order to estimate the assemblages' functional and phylogenetic diversity, we used the species traits (Appendix B: Table B.1) and the cladistic data (Appendix C: Table C.1) used by Doxa et al. (2016). The traits database is composed of twenty functional traits describing morphology, feeding strategy, defensive attributes, vertical distribution and ecological preferences of coralligenous species (Doxa et al., 2016; Tribot et al., 2016, Appendix B: Table B.2). The quadrats for which no cladistic data was available were not considered (16 quadrats).

2.3. Environmental and anthropogenic data

Using the 64 random points generated by CPCe (Kohler and Gill, 2006; Deter et al., 2012a, 2012b), we determined the percentage of sediment coverage by counting the number of points where sludge, rubble or sand were identified. This percentage of sediment coverage and depth are hereafter called environmental data. We used 13 anthropogenic pressures estimated on each station derived from Holon et al. (2015) and updated in 2018 by Andromède Océanologie (https://plateforme.medtrix.fr). These pressures ranged between 0 and 1 (0 = no pressure, 1 = maximum pressure) and include: agriculture, coastal engineering, urbanization, river inflows, erosion, industrial effluents, urban effluents, big boat anchoring, small recreational boating anchoring, maritime traffic and seaside tourism. To reduce the number of variables in our analyses, the information of these 13 anthropogenic pressures was synthesized into a unique variable through a Principal Component Analysis (Appendix D). Indeed, the first axis, mainly driven by professional fishing explained 64% of the variance in the 13 pressures. This proxy for anthropogenic pressures is thus hereafter named "exploitation".

2.4. Predictive model of aesthetic value

Tribot et al. (2016) conducted an online survey to evaluate the aesthetic preference of the public using 297 photographic quadrats of coralligenous reefs randomly chosen among the RECOR database. The 1260 participants were asked to choose from a series of pairs, the one they thought was the most beautiful. Once a high number of pairs had been evaluated, the Elo algorithm (Elo, 1978) was used to assign an aesthetic value to each quadrat. These evaluated photographic quadrats constituted the training dataset of the predictive model.

The aesthetic values of the 7692 photographic quadrats have been predicted with a deep learning algorithm. Deep learning algorithms are flexible enough to successfully process large datasets and have thus been largely used in various research fields including ecology mainly for identification or classification tasks (Christin et al., 2019). Another application of these algorithms is the prediction of continuous variables (Seresinhe et al., 2017; Lathuilière et al., 2018). We used Convolutional Neural Networks (CNN) that are particularly useful for computer vision tasks (Seresinhe et al., 2017; Lathuilière et al., 2018; Christin et al., 2019) such as classification or regression between the information contained in an image and a continuous variable (Lathuilière et al., 2018). The chosen strategy was to fine-tune a CNN pre-trained on ImageNet (Deng et al., 2010) to perform transfer learning. The good performances and ease of handling of the architecture of residual neural networks (ResNet) made them particularly relevant for our objective (He et al., 2015). Before training, the data set was split between training (207 quadrats), validation (60 quadrats) and testing (30 quadrats) sets. Due to the relatively small size of the dataset, data augmentation was needed to train the models. Photographic quadrats have been randomly rotated between −30 and 30 degrees and horizontal and vertical flips were applied randomly during each training iteration.

Considering the limited amount of data to train the network, we considered the two ResNet architectures that used the lowest number of parameters: ResNet18 and ResNet50. Both architectures were initialized with weights pre-trained on the ImageNet dataset, available via the *torchvision.models* function from *Pytorch v1.4.0*, and fine-tuned with our training set. The performances of the models were evaluated using the median absolute error (MedAE), the mean absolute percentage error (MAPE) and the R^2 of the linear regression of the predicted values against the evaluated values. Once the best hyperparameter configuration had been selected for both models using the validation set, the ResNet50 was finally retained as the best performing model on unseen photographic quadrats: the testing set. The fine tuning of the predictive model and the predictions of the aesthetic values were performed with *Python 3.7*, *Pytorch 1.4.0* and *torchvision 0.5.0*. Once the aesthetic values of all photographic quadrats were obtained, the aesthetic value of each station was computed as the mean value of all the quadrats sampled at this station over time (same latitude, longitude and depth).

2.5. Biodiversity analysis

Considering the multiple facets of biodiversity is important to estimate the ecological values of ecosystems (Reiss et al., 2009). To do so we computed taxonomic (species richness), functional (ecological roles) and phylogenetic (evolutionary history; Cadotte and Davies, 2010) distances (Chao et al., 2014) between species within a single assemblage (quadrat). To include information on species abundances we used the Hill approach which was originally proposed for taxonomic diversity (Hill, 1973) and recently generalized to functional and phylogenetic diversity metrics (Chao et al., 2014, 2019). The Hill approach has the advantage of proposing a continuous measure of diversity without the need to make any *a-priori* decision on the relative importance of species abundance or their pairwise distance. It can shift from equal importance (number of species) to uneven importance (such as in Shannon entropy and Simpson index, Magurran 1988) by modifying a single parameter *q*.

Generalized Hill numbers are expressed in number of equivalent units: the effective number of taxonomic (species), functional (species pair of unit distance) or phylogenetic (branch of unit length) entities in the studied assemblages. Here, pairwise distance between species were computed in the functional space of the assemblage (computed with the functional traits and the dist.ktab function of the ade4 package; Pavoine et al., 2009) and branch lengths were determined using cladistic information. Generalized Hill numbers ($qD\left(\overline{V}\right)$) were computed applying the following equation (Chao et al., 2014, Table 1):

$$qD\left(\overline{V}\right) = \left[\frac{qAD(\overline{V})}{\overline{V}}\right]^{\frac{1}{\lambda}} \tag{1}$$

where $\lambda = 1$ for taxonomic and phylogenetic diversity or $\lambda = 2$ for functional diversity,

$$qAD\left(\overline{V}\right) = \left[\sum\nolimits_{u=1}^{C} v_u \times \left(\frac{a_u}{\overline{V}}\right)^q\right]^{\frac{1}{(1-q)}} \tag{2}$$

and

$$\overline{V} = \sum\nolimits_{u=1}^{C} v_u a_u \tag{3}$$

In Eqs. (2) and (3), u is an element of the collection C(a species for taxonomic diversity, a species-pair for functional diversity, a branch segment for phylogenetic diversity), v_u is the attribute value (unity, pairwise distance, branch length) and $a_u$au is the relative abundance of an entity. In Eqs. (1) and (2), the parameter q defines the sensitivity of the diversity value to species relative abundance. For $q = 0$, the Hill number is species richness. For $q < 0$ more importance is given to rare species whereas for $q > 0$ more importance is given to dominant species. For $q = 1$ and $q = -1$, equal importance is given to species relative abundance and to the pairwise distances. The taxonomic, functional and phylogenetic diversities are hereafter respectively named qTD, qFD and qPD. In our analysis, as our focus is on the relationship between the aesthetic value and the different biodiversity metrics, we varied the parameter q between -1 and $+1$ for each metric and selected the q value that maximized the R^2 of the regression between the aesthetic value and the Hill number (using log transformation). Following the recommendations in Chao et al., 2019, τ the threshold of functional distinctiveness was set to d_{mean}, the mean functional distance between any two randomly selected species.

Note that by construction functional (qFD) and phylogenetic (qPD) diversities are correlated to taxonomic diversity (qTD). To produce estimates for qFD and qPD independent of taxonomic diversity we used a null-model algorithm (Harvey et al., 1983; Ulrich and Gotelli, 2010) called "*r2dtable*" designed to generate abundance matrices conserving the total sum of the cells of the matrix as well as the column and row sums. For both qFD and qPD, 1000 random abundance matrices were generated to reach asymptotic stability and guarantee the statistical validity of the process. Relative abundances were then computed and finally, a SES (Standardized Effect Size, Botta-Dukát, 2018) value of the index was obtained for each assemblage by standardizing the observed value using the distribution of null values according to the following equation:

$$SES_X = \frac{X - \mu}{\sigma} \tag{4}$$

where X the index computed on the real assemblage, μ and respectively the mean and standard deviation of the 1000 simulated indices for each of the null assemblages. The resulting functional and phylogenetic corrected diversities are noted qFD_{SES} and qPD_{SES}.

Finally, we estimated the contribution of each species (or taxonomic entity) to the aesthetic value of the photographic quadrats. Using multiple linear regression modelling, we quantified the variation of the aesthetic value explained by the relative abundance of individual species to rank the species according to the strength of their effect on the aesthetic value. To ensure convergence and stability of the model, the species identified on less than five quadrats were not considered in this analysis (removing 31 species). First, the relative abundance of each individual species, ordered by their independent contribution to the total variation in the response variable, were entered in a linear model explaining the aesthetic value. A sequential backwards selection procedure permitted to remove non-significant terms and to obtain a minimal adequate model. The coefficients of this final model were used to assess the contribution of each taxonomic entity to the aesthetic value.

Functions from the R package *hillR* were adapted to compute the Hill numbers and select the best *q* parameter. The R packages *ape v.5.5* and *ade4 v.1.7–16* were respectively used for the phylogenetic and functional diversity. The R packages *vegan v.2.5–7*, *stats* (attached to base) and *PerformanceAnalytics v.2.0.4* were used to compute the SES.

2.6. Modelling influence of biodiversity, environmental variables and anthropogenic pressures on the aesthetic value

Because biodiversity, environmental variables and anthropogenic pressures were expected to have combined effects on the aesthetic value and potential indirect interactions, we used Structural Equation Modelling (SEM) to compare the different effect paths that can be envisioned to formalize these causal relationships (Grace et al., 2010). A SEM is a regression method estimating the plausibility of a pool of

Table 1
Metrics of the two architectures of deep learning algorithms used (ResNet18 and ResNet50).

	Validation set (60 quadrats)			Test set (30 quadrats)		
Model	MedAE	MAPE	R^2 score	MedAE	MAPE	R^2 score
ResNet18	45.5	3.71	0.74	–	–	–
ResNet50	38.49	3.31	0.79	33.49	3.04	0.83

relationships between a defined set of variables. Here, all variables being measured (not latent), we performed a confirmatory path analysis constructed as a d-step test based on independence between variables (Shipley 2009). To reject or not a hypothetical model, the (k) supposed relations of independence must be evaluated. Each claim of independence is assigned a probability (p_i) and the combination of those gives a value, C (Equation (5)). To validate the hypothetical model, C must follow a chi-squared distribution with 2 k degrees of freedom.

$$C = -2\sum_{i=1}^{k} ln(p_i) \quad (5)$$

The analysis was performed at the quadrat level (7692 quadrats). The structure of the initial model implied only unidirectional relationships between variables, starting from depth to aesthetic value through anthropogenic pressures, environmental variables and diversity metrics, implying a high number of independence claims. Successive models were tested, adding relationships between the variables when they were unlikely to be independent.

The confirmatory path analysis was led among quadrats using seven variables: the aesthetic value, qTD, qFD_{SES}, qPD_{SES}, percentage of sediment coverage, depth, and exploitation pressure (Appendix E). As our dataset is hierarchized (two quadrats of the same station are more likely to be similar than two quadrats of different stations and two stations of the same site are more likely to be similar than two stations of different sites) we had to take into account pseudo-replication. Stations and sites were thus considered as random effects in the hypothetical models with stations nested within sites (Bunnefeld and Phillimore, 2012).

We used the *lmer* function of the *lmerTest v.3.1–3* R package and the *cfa* function of the *lavaan v.0.6–7* R package to compute the SEM and the function *ChordDiagram* of the *circlize v0.4–10* R package to visualize it.

2.7. Mapping aesthetic and ecological values

In order to compare aesthetic and ecological gradients, we computed a synthetic estimate referred to as “ecological value” that gathers the three facets of biodiversity. To build this index, the quadrats were ranked thrice according to qTD, qFD_{SES} and qPD_{SES}. The three ranks were summed and used to rank the quadrats one more time. This final rank was used as a proxy for the ecological value of a quadrat: the smaller the rank, the higher the ecological value. Using ranks presents the advantage that all differences, intra-value and inter-values are expressed homogeneously with a common unit value. This composite metric thus gives equal weights to TD, qFD_{SES} and qPD_{SES}. We also ranked the quadrats according to their aesthetic values (the smaller the rank, the higher the aesthetic value) so we were able to use a Kendall test

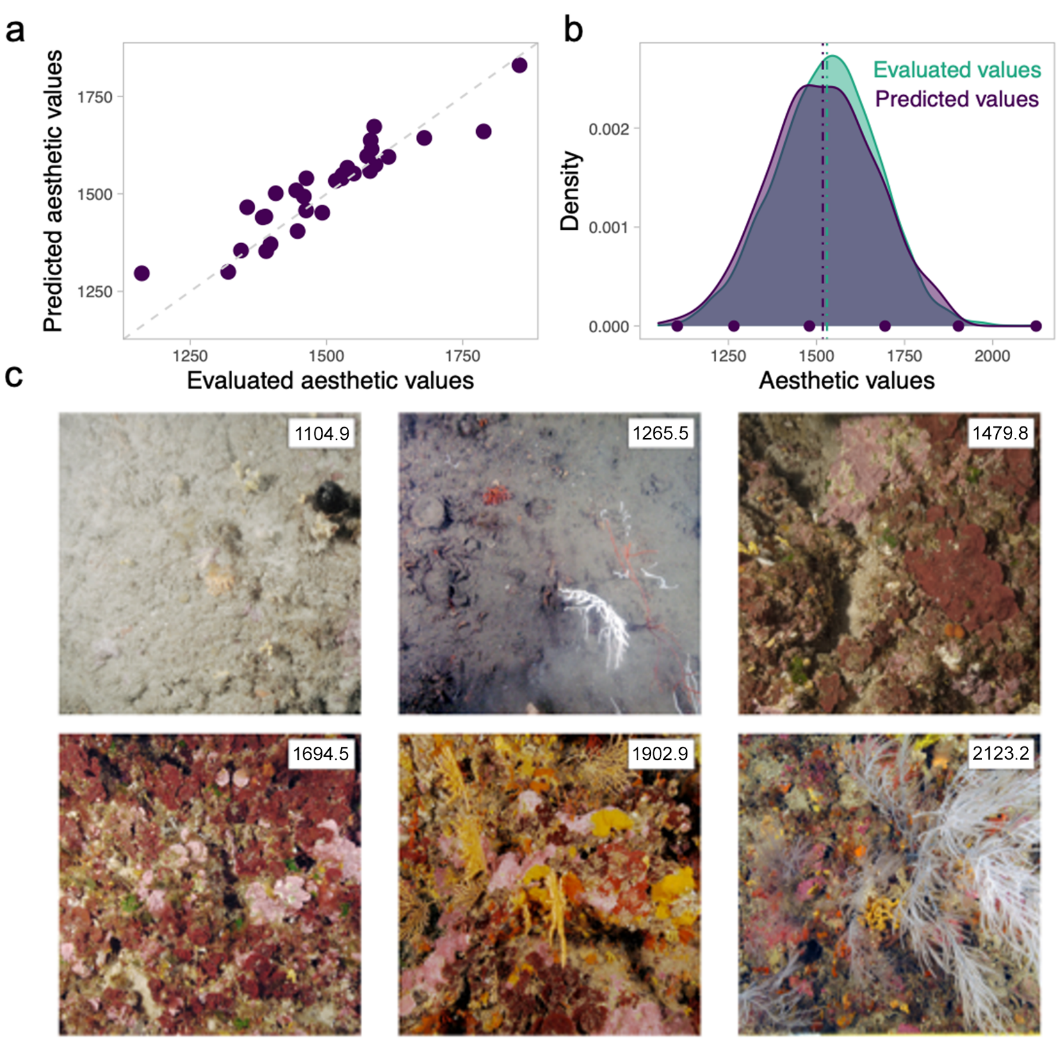

Fig. 2. Performances of the deep algorithm (a) Linear regression between the evaluated aesthetic values of the test set and the values predicted by the deep algorithm for this dataset ($R^2 = 0.83$). (b) Distribution of the predicted values for the 7692 photographic quadrats of the database (purple) and the evaluated values from Tribot et al. 2016 (green). (c) Examples of photographic quadrats with contrasted aesthetic values along the gradient of predicted aesthetic values (points on the x axis of panel b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Kendall 1938) in order to evaluate the correlation between ecological and aesthetic values at the quadrat level. To summarize the information on a map, both the aesthetic and the ecological values were averaged at the station level. As coralligenous reefs are not continuously distributed along the French Mediterranean coastline nor along the water column, our map represents each station as a discrete point located according to its longitude, latitude and depth.

3. Results

3.1. Predictive model of aesthetic value

The best performances obtained for the ResNet18 and ResNet50 were respectively MedAE = 45.4, MAPE = 3.71, R^2 = 0.74 and MedAE = 38.49, MAPE = 3.31, R^2 = 0.79 (Table 1). Considering the results of the ResNet50, the performances were slightly higher for the test set (R^2 = 0.83) than the validation set (R^2 = 0.79).

The R^2 of the linear regression of the predicted values against the Elo evaluated values for the testing set (30 photographic quadrats) was 0.83 (Fig. 2a). The aesthetic values for all the 7692 photographic quadrats of our database were then predicted using the trained model and range from 1051.1 to 2123.2 (mean value = 1529.6, standard deviation = 145.4) (Fig. 2b). The shape of the distributions of the previously evaluated values in Tribot et al. (2016) and of the predicted values were not different (Kolmogorov-Smirnov test, D = 0.06, p-value = 0.20). The gradient of aesthetic value obtained is illustrated by the photographic quadrats presented on Fig. 2c.

3.2. Biodiversity analysis

3.2.1. Biodiversity metrics

Before computing the different biodiversity metrics, we computed a multivariate analysis on the functional traits. The first axis (24.7%) of the functional space of the 177 species was mainly positively driven by the traits 'coralligenous builder', 'colonial', and 'consistency'. The second axis (16.8%) was mainly driven negatively by the traits 'base type' and 'colonial' and positively by the trait 'coralligenous builder' (Appendix B: Fig. B.1).

Taxonomic, functional and phylogenetic diversities (respectively noted TD, FD and PD) of each quadrat were computed with information on species abundances. We selected the parameter q of Eq. (2) that maximized the correlation between each of the biodiversity facets and the aesthetic values (Appendix F: Fig. F.1). We found respectively $q = -1$ for TD ($R^2 = 0.17$), $q = -1$ for FD ($R^2 = 0.10$) and $q = -1$ for PD ($R^2 = 0.11$) and computed qTD, qFD and qPD accordingly. We finally produced estimates for qFD and qPD independent of qTD using a null-model

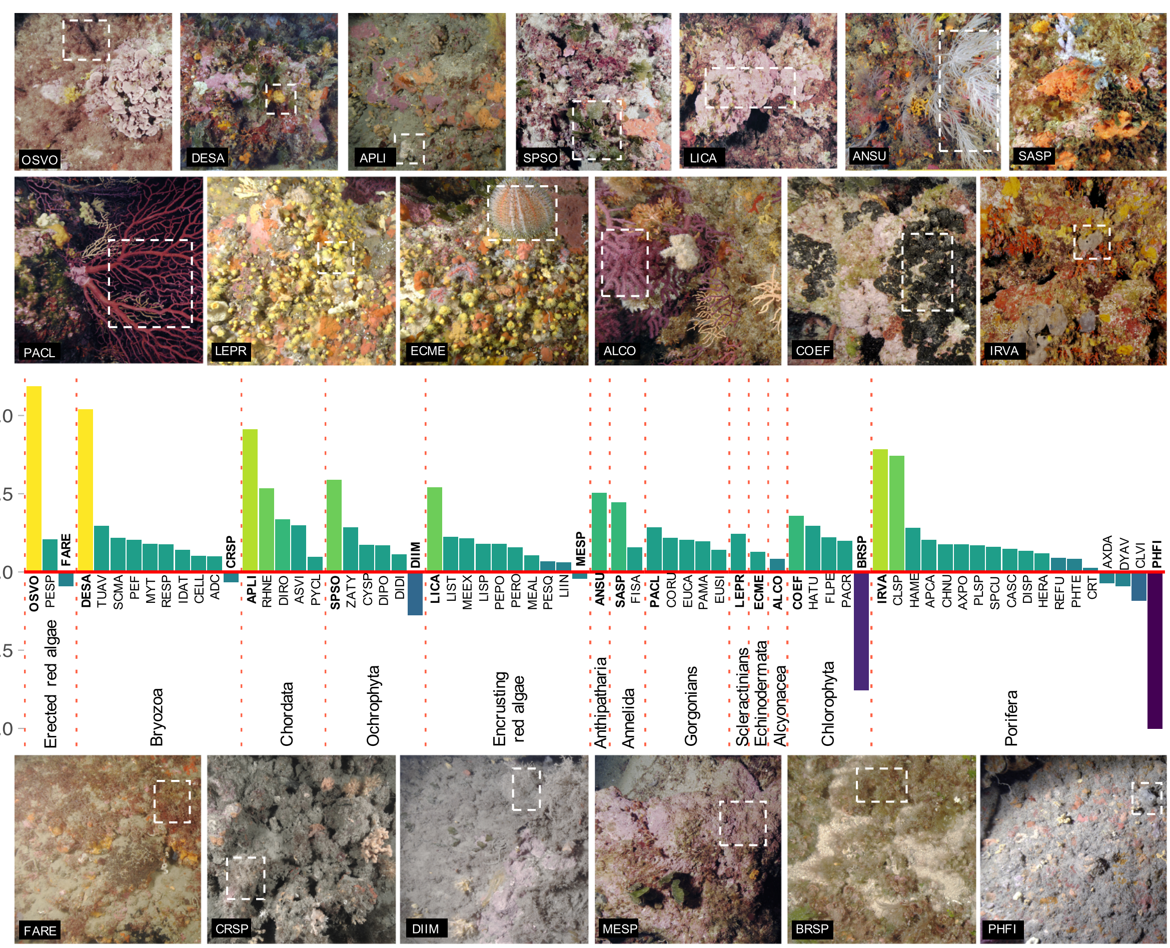

Fig. 3. Effect of the species composition on the aesthetic value: Histogram of the strength (and direction) of the significant ($p < 0.05$) effects of 68 species on the aesthetic values of the photographic quadrats (coefficient associated to each species in the linear model between the aesthetic value of the photographic quadrats and the relative abundances of the species). For each taxonomic group, we show examples of photographic quadrat which contain the species with the highest positive (above) and/or the lowest negative (below) effects on the aesthetic value (illustrated by the white dashed rectangles). The corresponding names of those species are OSVO = *Osmundaria volubilis*; FARE = *Gloiocladia repens*; DESA = *Dentiporella sardonica*; CRSP = *Crisia sp*; APLI = *Aplidium sp*; SPSO = *Spatoglossum solieri*; DIIM = *Dictyota implexa*; LICA = *Lithophyllum cabiochae*; MESP = *Mesophyllum sp*; ANSU = *Antipathella subpinnata*; SASP = *Sabella spallanzanii*; PACL = *Paramuricea clavata*; LEPR = *Leptopsammia pruvoti*; ECME = *Echinus melo*; ALCO = *Alcyonium coralloides*; COEF = *Codium effusum*; BRSP = *Bryopsis sp*; IRVA = *Ircinia variabilis*; PHFI = *Phorbas fictitius*. For the other species (not in bold on the figure), please refer to Appendix F.

approach and found qFD_{SES} values ranging from −10.08 to 2.97 (mean qFD_{SES} = −2.70) and qPD_{SES} ranging from −10.08 to 3.49 (mean qPD_{SES} = −2.79) (Appendix F: Fig. F.2). The distribution of qFD_{SES} was slightly left tailed with a skewness of −0.68. This suggests that functional diversity within quadrats was lower than expected by chance, regardless of the species richness. The distribution of qPD_{SES} was slightly right tailed with a skewness of 0.14 suggesting that phylogenetic diversity within the quadrat was slightly higher than expected by chance, regardless of the species richness.

3.2.2. Effect of species composition on the aesthetic value

As shown by Tribot et al. (2016), we expected certain species to have a significant positive or negative impact on the aesthetic value of quadrats. Indeed, 68 of the 177 species identified in the entire database had a significant impact on the aesthetic value (Fig. 3). Overall, the relative abundance of these 68 species explained 31.4% of the variance in the aesthetic value. The direction and strength of the effect of a species is given by the associated slope in the linear model. Fifty-nine species had a significant positive effect (mean = 0.27). *Osmundaria volubilis* (1.19), *Dentiporella sardonica* (1.04) and *Aplidium sp* (0.91) were the three species with the highest positive effects Appendix F). Only nine species had a significant negative impact on the aesthetic value (mean = −0.29). *Phorbas fictitius* (−1.00) and *Bryopsis sp* (−0.76) were the two taxonomic entities with the highest negative effects (Appendix G).

3.3. Influence of biodiversity, environmental variables and anthropogenic pressures on the aesthetic value

After testing successive hypotheses, the selected Structural Equation

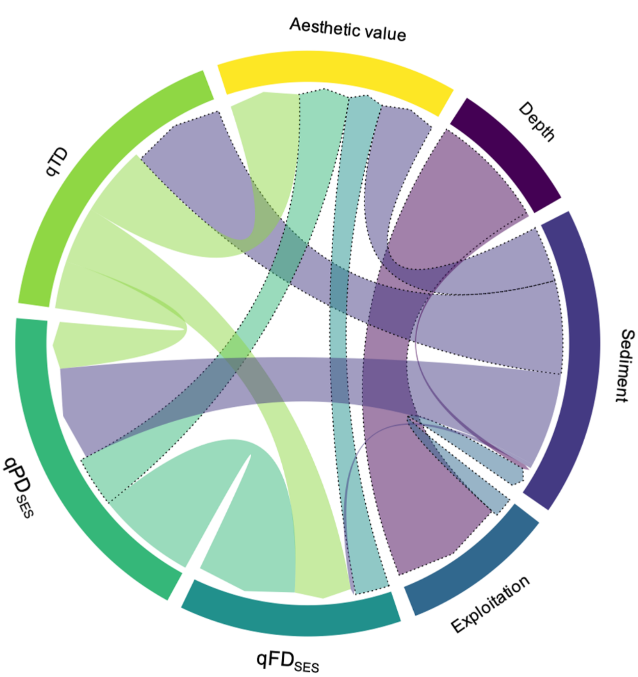

Fig. 4. Chord chart summarizing the interactions between the aesthetic value, qTD, qFD_{SES}, qPD_{SES}, the percentage of sediment cover, depth and the first axis of the PCA on the 13 anthropic threats. All variables have been computed or aggregated at the station level. Each link is colored according to the variable it comes from and its destination is indicated by the end of the arrow. The width of the arrow is proportional to the contribution of the explaining variable to the percentage of the dependent variable explained in the whole model. The length of the arc of the circle representing a variable is the sum of the width of the links coming from and arriving at this variable. The arrows with plain (respectively dotted) edges represent positive (respectively negative) contributions from the explaining variable to the dependent variable.

Model (SEM) included the highest number of independences claims not rejected by the chi-squared test ($C = 18.4$, 16 degrees of freedom; Fig. 4; see Appendix E for the equations of the model). Considering the relationships not rejected by the chi-squared test, 25.4% of the variance in the aesthetic value was explained by qTD, qFD_{SES}, qPD_{SES} and the percentage of sediment coverage. 11.2% of the variance in qTD was explained by the percentage of sediment coverage. 23.7% of the variance in the qPD_{SES} was explained by qTD and the percentage of sediment coverage. 44.9% of the variance in the functional diversity was explained by qTD, qPD_{SES} and the percentage of sediment coverage. 18.6% of the variance in the exploitation pressure was explained by depth. Depth and exploitation explained 1.1% of the variance of sediment coverage while depth itself was independent from the other considered variables (Table 2, Fig. 4). More specifically, concerning the aesthetic value we found that qPD_{SES}, qFD_{SES} and the percentage of sediment coverage had limited negative effects (respectively −0.14, −0.07 and −0.17) while qTD had a strong positive effect (0.40).

3.4. Mapping the aesthetic and ecological values

We aimed at identifying the relationships between the aesthetic and ecological values and mapping their spatial distributions along the French Mediterranean coastline. To do so we quantified the ecological value by synthesizing the information on qTD, qFD_{SES} and qPD_{SES} for each quadrat (Appendix H). The quadrats have also been ranked according to their aesthetic value in order to compare it to the ecological value. A Kendall test showed a low but significatively positive correlation between aesthetic values and ecological values ($\tau = 0.044$, p-value < 0.001) (Fig. 5).

Each station had been represented on the map (Fig. 6) as a circle at its longitude, latitude and depth. The color of each point represented the mean aesthetic value of the station which ranged from 1214.2 to 1729.3 while the size of the point represented the ecological value of the station which ranged from 1149.4 for the station with the higher ecological rank to 6300.3 for the station with the lower ecological rank. The relationship between the aesthetic and ecological values at the station level was not significant ($\tau = 0.053$, p-value = 0.32) (Fig. 6c). The mean aesthetic and ecological values of the stations were respectively 1506.3 (±117.8) and 3826.1 (±1190.5) for the mainland, 1526.7 (±92.1) and 3554.9 (±1042.8) for Corsica. There was no clear pattern in the distribution of each variable along latitude, longitude or depth but in Corsica, there were less stations of low aesthetic value (Fig. 6b, Kruskal-Wallis test: $\chi^2 = 9.12$, p-value = 0.03).

4. Discussion

Using coralligenous reefs as a case study, we propose an estimation

Table 2
Percentage of explained variance for each variable included in the SEM and detail of the coefficients corresponding to each explaining variable.

Dependant Variable	Explaining Variable	Coefficient	% of explained variance
Aesthetic Value	qTD	0.40	25.4%
	qPD_SES	−0.14	
	qFD_SES	−0.07	
	Sediment	−0.17	
qTD	Sediment	−0.33	11.2%
qPD_SES	qTD	0.29	23.7%
	Sediment	0.50	
qFD_SES	qTD	0.34	44.9%
	qPD_SES	0.53	
	Sediment	0.06	
Exploitation	Depth	−0.43	18.6%
Sediment	Depth	0.10	1.1%
	Exploitation	−0.01	
Depth	–	–	–

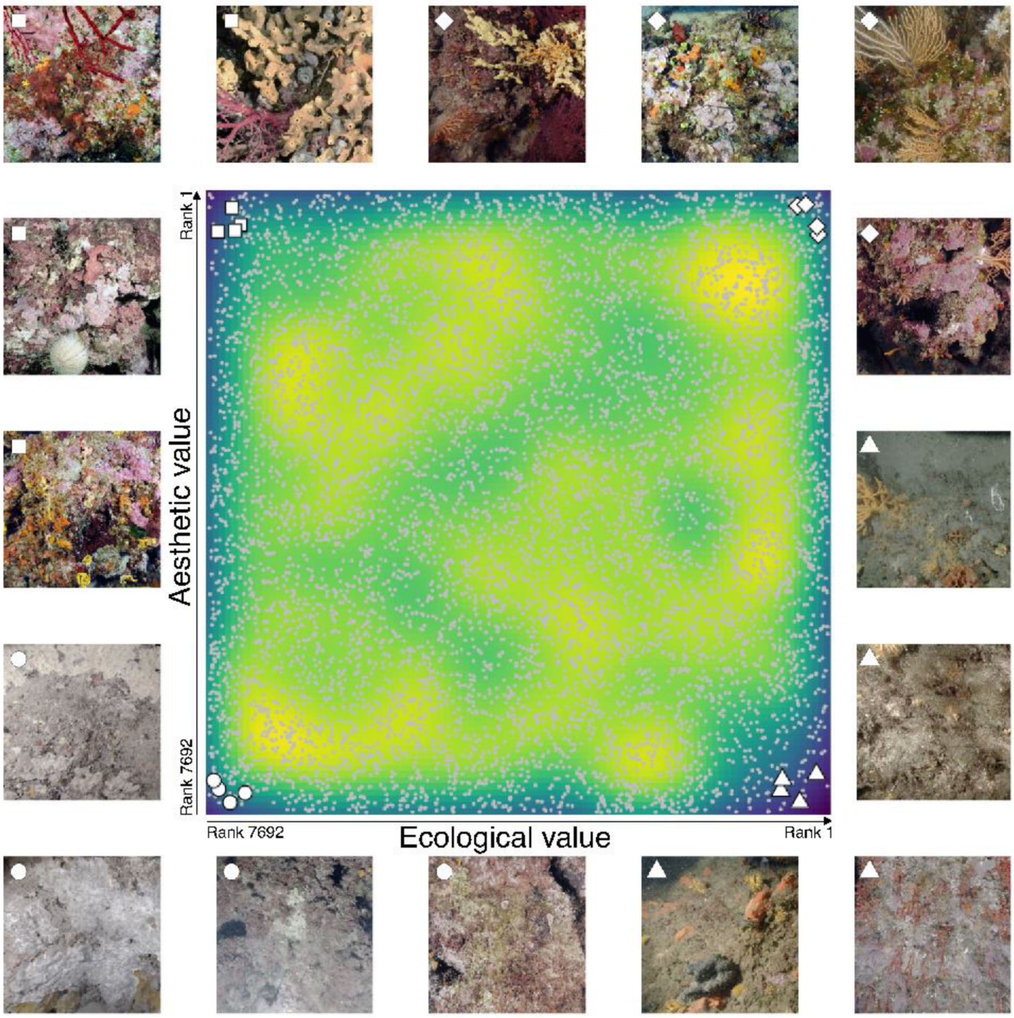

Fig. 5. The correlation between the aesthetic and the ecological values of the photographic quadrats is low but significatively positive (Kendall test τ = 0.044, p-value < 0.001). The quadrats are ranked increasingly (the smaller the ranks, the higher the values). The photographic quadrats on the edges of the graph are examples of four extreme situations: high aesthetic but low ecological values (squares), high aesthetic and high ecological values (diamonds), low aesthetic but high ecological values (triangles), low aesthetic and low ecological values (rounds).

of aesthetic value combining a quantitative evaluation of human perception and deep-learning algorithms. The deep-learning approach allowed us to predict the aesthetic value of 7692 photographic quadrats. This aesthetic value estimation was then compared with multiple facets of biodiversity, environmental variables and anthropogenic pressures to illustrate the main drivers of human preference for this endangered ecosystem and mapped along the French Mediterranean coastline.

4.1. Using convolutional neural networks to predict the coralligenous aesthetic value

Using a training set of 297 photographic quadrats evaluated through online questionnaires (Tribot et al., 2016), we trained a deep learning algorithm that successfully predicted aesthetic value of coralligenous quadrats. Surprisingly, the R^2 of the testing set containing 30 quadrats (0.83), was higher than the R^2 of the validation set that contains 60 quadrats (0.79). The median absolute error (MedAE) was higher for the validation test (38.49, Table 1) than for the test set (33.49, Table 1) which suggested that the model might make slightly larger mistakes (predict scores slightly more different than the evaluated ones) in the validation set than in the test set. However, the differences were small enough to call the performances consistent, indicating good generalization capabilities (Hastie et al., 2009). Overall, the predictive power of our deep learning algorithm ($R^2 = 0.83$, Fig. 2a) was high and allowed us to predict the aesthetic value of the 7692 quadrats of our photographic database with good confidence. These performances confirm the good transferability of pre-trained weights on the ImageNet data set. The predictive capacities of the algorithm give no indication on why a particular photographic quadrat would have a better aesthetic value than another but previous studies have shown that color heterogeneity and variation in luminosity and saturation are the main drivers of aesthetic response for this particular ecosystem (Tribot et al., 2016) as well as for coral reef ecosystems which are visually closely related (Haas et al., 2015) but also for marine tide pool ecosystems (Fairchild et al., 2018).

Beyond this present study, the deep learning predictive algorithm we developed for coralligenous photographic quadrats offers many new opportunities among which, the possibility to extend the prediction of aesthetic value to other sets of coralligenous photographic material. Using photographic quadrats is indeed among the most common techniques to survey coralligenous reefs (*e.g.* Kipson et al., 2011; Deter et al., 2012a, 2012b; Casas-Guëll et al., 2016; García-Gómez et al., 2020) but recent techniques including videos recorded by underwater robots (e;g. Appolloni et al., 2020) could also increase the amount of material available. After new calibration and training, such a large and heterogeneous dataset could allow us to apply our methodological framework to different sources of photographic material. However, extending our framework to global evaluation of coralligenous reefs also raises the question of the scale transferability of our trained neural network from quadrats (50 × 50 cm in our study) to coralligenous seascapes. The good correlation we found between the aesthetic value of the quadrats and the averaged values at the station level (Appendix I) gave us good

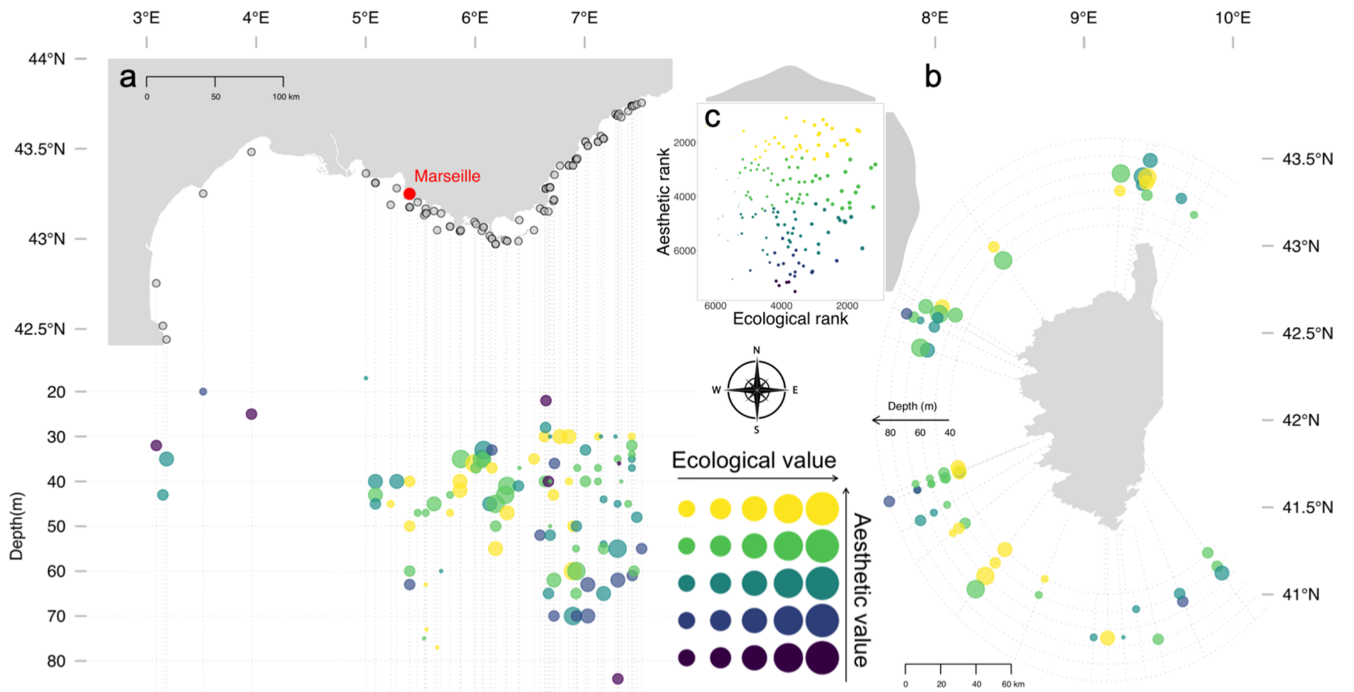

Fig. 6. (a) and (b) Map of the aesthetic value and ecological value of the stations of coralligenous reefs of the French Mediterranean coastline. (c) Relation between the aesthetic rank and the ecological rank and their distribution on the edges of the figure. The Kendall test between the two gives $\tau = 0.053$ with a p-value $= 0.32$. The size of the circles is determined by the ecological value of the station while the color is based on the aesthetic value.

confidence that this scaling up is possible. New investigations involving human evaluation of the aesthetic value of larger portions of coralligenous reefs will be needed before going further along this line. Beyond coralligenous reefs we also believe that the neural network we trained on coralligenous images could be used as a basis to train other convolutional neural networks dedicated to coral reefs images and provide an efficient and novel tool to evaluate the aesthetic value of tropical coral reef ecosystems of which millions of images are available on the web, in social media and in the scientific literature (Haas et al., 2015). This transfer to coral reef ecosystems will need to conduct new online surveys to collect enough material to train the convolutional neural networks, but we see here a strong opportunity for transfer learning from what we have done with the coralligenous dataset.

4.2. Biological and anthropogenic drivers of aesthetic value

4.2.1. Multiple facets of biodiversity

Biodiversity descriptors based on taxonomic diversity alone (species richness and abundances) are not fully adapted to conservation biology and other descriptors such as functional and phylogenetic diversity must also be taken into account (Reiss et al., 2009; Mouquet et al., 2012; Winter et al., 2013). In order to estimate the taxonomic, functional and phylogenetic diversity we choose to compute Hill numbers (Chao et al., 2014). Here, we used a strategy without any a priori fixed value for the q parameter, varied q between -1 and $+1$ and picked for each diversity facet the q value that maximized the correlation between each metric and the aesthetic value. We found that negative q values were maximizing the three fits which indicated that the aesthetic value was more correlated to a diversity metric that gives more weight to rare species than abundant ones (Chao et al., 2014). Altogether these results suggested that the species composition is more important than abundances in explaining high aesthetic values. For instance, *Dentiporella sardonica,* the bright and yellow small, erected bryozoan mentioned before, had an average relative abundance of 5% (reaches 10% in one quadrat) but had a significant positive effect (Fig. 3, Appendix G) whereas *Phymatolithon calcareum,* an unattached red coralline alga, had an average relative abundance of 41% (reaches 100% in several quadrats) had no significant effect on the aesthetic value. For these two species, their relative size was more important than their abundance within each quadrat. This qualitative rather than quantitative influence of species diversity on the aesthetic value corresponds to what was previously described on coralligenous reefs by Tribot et al. (2016) and on tide pool ecosystem by Fairchild et al. (2018). Altogether these results echo with the 'grouping and binding' rules of aesthetic experience (images where humans can group patches or delineate objects from the background are more appreciated) defined in neuroaesthetics (Ramachandran and Seckel, 2012; Chatterjee and Vartanian, 2014). Indeed, in our photographic quadrats, very large and distinct species (for instance *Antipatharia* or *Gorgonians*) contributed highly to the aesthetic value of quadrats (Fig. 3).

To obtain estimators of the functional and phylogenetic diversity independent from the taxonomic diversity, we computed standardized effect size indices (Botta-Dukát 2018). We found that the distribution of qFD_{SES} (respectively qPD_{SES}) was left (respectively right) tailed meaning that the functional diversity (respectively phylogenetic diversity) observed in the quadrats was lower (respectively higher) than what was expected by chance. Overall, the 7692 quadrats are spread among 160 stations between 20 and 90 m depth gathered on 95 sites along the French Mediterranean coastline. This diversity of depths and geographical positions covers a very heterogeneous gradient of environmental conditions and human pressures which might explain this filtering of functional and phylogenetic diversities, as under (respectively over) dispersion can be expected when environmental filtering is strong (Cavender-Bares et al., 2009).

4.2.2. Species composition

We found that the combined effects of 68 species explained 31.4% of the variance in the aesthetic value illustrating the significant impact of some species (Fig. 3). Tribot et al. (2016) showed that some paraphyletic groups have a significant positive impact on the coralligenous aesthetic value (green algae, *gorgonians* and corals, sea urchins and *bryozoans*). The extent of our study allows us to deepen this result as we found that while some groups have overall positive effects on the aesthetic value such as *Chordata* (*e.g. Aplidium* sp, transparent social ascidians organized in bouquets), or *gorgonians* (*e.g. Paramuricea clavata* a red or yellow colonial soft coral), some others contain species with both positive and negative effects. For instance, in the group of *bryozoans*, *Dentiporella sardonica* (a bright, yellow, small, erected *bryozoan*) has a positive effect while *Crisia sp* (white or yellow *bryozoan* shrubs) has a negative effect. Interestingly most of the species' effects were positive and only nine species had negative effects. The three species with the strongest negative effects were *Phorbas fictitius* (a sponge which forms thin sheets of color grey or pale orange pink), *Bryopsis sp* (green algae, in tufts) and *Dictyota implexa* (a small pale-yellow algae). Most of the species with negative effects have in common that they are encrusting or close to the substrate and sciaphilous or at least shade tolerant. Note also that some of these species are found in degraded environments which makes it difficult to estimate their individual contributions to the aesthetic value (Fig. 3). Indeed, one of the limits of the species composition effect analysis is that indirect effects (association between species) and/or direct effects of the environment (if a species is often found on a degraded reef with a low aesthetic value it will show a negative effect) can blur the result of the analysis. For instance, *Sabella spallanzanii,* a *polychaeta* worm whose crown of tentacles are always retracted into its sandy tubes on the photographic quadrats (and thus are often not visible), showed a strong positive effect but is probably associated with other species that have direct positive effect (it is barely visible on the photographic quadrat as illustrated in Fig. 3). *Axinella damicornis* however, a yellow crumpled sponge found on muddy funds and rocky faces, is often covered with encrusting anemones or sediment, hiding it from sight (Göthel 1996). Despite these limitations 59 species (over 177) had a positive effect on the aesthetic value which highlighted the overall positive effect of biodiversity composition on coralligenous aesthetic value going beyond the taxonomic diversity effect.

4.2.3. Global relationships between the aesthetic value, biodiversity metrics, environmental variables and anthropogenic pressures

The structural equation modelling (SEM) approach allowed us to explore the combined effects of the three facets of biodiversity, anthropogenic pressures and environmental variables on the aesthetic value. Note that the SEM analysis provided a powerful but complex set of information on the relationships between all the variables considered in our analysis. As we are mainly concerned with aesthetic value, we will focus our interpretation on the direct and potential indirect effects of the different variables on the aesthetic value.

Our results showed that 25.4% of the variance in the aesthetic value was explained by the variables included into our SEM analysis. We found a direct negative effect of sediment on the aesthetic value. The sediment present on coralligenous reefs (sludge, rubble and sand) covers the species and homogenizes the photographic quadrats' colors which reduces the aesthetic experience. Indeed, the negative effects of sediment directly impacted taxonomic diversity thus has an additional indirect effect on the aesthetic value. Confirming previous results (Tribot et al., 2016), we found that taxonomic diversity has a strong positive impact on the aesthetic value. As the coralligenous species accumulates they combine colors and shapes that are appealing to humans and increase its aesthetic value (Chatterjee and Vartanian, 2014). The SEM approach, by taking into account indirect effects between variables, showed however contrasted effects of phylogenetic and functional diversities on the aesthetic value compared with what was previously thought (Tribot et al., 2016; Fairchild et al., 2018). Indeed, we found both negative effects of standardized phylogenetic and functional diversities on the aesthetic value (despite the positive effect of taxonomic diversity on these two variables). As qPD_{SES} and qFD_{SES} were highly correlated (Appendix H) we assume that the presence of both phylogenetically and functionally distant species lowers the aesthetic value of the coralligenous. This effect is probably linked to the presence of Chlorophyta such as *Bryopsis* marine algae that can form dense and dark green tufts. Their presence increases both the phylogenetic and functional diversities when associated with coralligenous fixed marine animals and lowers the aesthetic value. This negative effect was not found by Tribot et al. (2016) who worked on a much lower number of photographic quadrats and thus might not have accumulated enough information on species diversity to show this effect. Fairchild et al. (2018) used a SEM analysis and found a direct positive effect of functional diversity (and indirect positive effect of phylogenetic diversity) on human interest for tide pool communities but as they used only animal taxa, they might have missed the larger phylogenetic resolution that explains the net negative effect we found here. Our results have important implications as most of the studies linking biodiversity to aesthetic value found either positive or null relationships (Tribot et al., 2018a, 2018b for a review). Here we show that there is a strong and positive effect of taxonomic diversity on the aesthetic value but that once the phylogenetic and functional diversities are standardized by species richness their impact is negative. Even if we believe that this result is not generalizable as it depends on the system studied and the phylogenetic resolution considered, it highlights that the relationship between the different facets of biodiversity and the aesthetic value is more complex than initially thought (Graves et al., 2017; Tribot et al., 2019). This negative effect of functional diversity on aesthetic values was suggested in a previous study at the species level by Tribot et al. (2018a), Tribot et al. (2018b) that found that beautiful coral reef fishes were less functionally distinct than less beautiful fishes. This finding echoes our results and suggests a potential bias in the human perception of biodiversity: what the public finds beautiful is not necessarily ecological functionally diverse.

Interestingly we found no effect of human pressure (Exploitation) on biodiversity nor on the aesthetic value. This result was a bit surprising but can be explained by the nature of the data we used to estimate human pressures. Indeed, the pressures were computed as a decreasing function of depth: the value diminishes by 10% every 10 m (Holon et al., 2015). As the majority of the stations are below 30 m deep up to 90 m (Fig. 6) the pressures used in our analysis were highly attenuated. Note also that in our data, "Exploitation" was mainly driven by professional fishing and did not account for trawling fishing methods, recreational fishing, and spearfishing which are known to damage coralligenous reefs at various depths (Deter et al., 2012a, Rastorgueff et al., 2015, Holon et al., 2015, Ferrigno et al., 2017). These data were not available at the large scale we used for our study but should be taken into account in future studies and are likely to increase the negative impact of anthropogenic pressures on coralligenous diversity, and indirectly on its aesthetic value.

4.3. Mapping the aesthetic and ecological values of the coralligenous reef along French Mediterranean coastline

We developed a synthetic index to estimate ecological value (see Section 2.7) which has the advantage to give equal weights to taxonomic, and standardized functional and phylogenetic diversities (qTD, qFD_{SES} and qPD_{SES}). At the quadrat level we found a significant positive relationship between ranked aesthetic and ecological values which indicates that, overall, the most appealing coralligenous quadrats are of higher ecological values. However, as expected from the SEM analysis, this correlation, even if significant, was weak (Fig. 5) and we found some quadrats of high (respectively low) aesthetic values with low (respectively high) ecological values. This heterogeneity confirms that human aesthetic preference is not always associated with healthy coralligenous reefs (see also Vercelloni et al., 2018). By construction a low or high ecological value can correspond to different combinations of taxonomic, phylogenetic and functional diversities (which, we agree, is a limitation of our ecological value estimate). However, a closer look at the photographic quadrats on the extreme of the aesthetic/ecological gradients gives some insights on the source of this heterogeneity (Fig. 5). For instance, quadrats with low species number or with species closely related both on phylogenetic or functional dimensions (Fig. 5, squares) but with colorful and erected species (such as *Aplysina cavernicola* a yellow erected sponge or *Paramuricea clavata* the violescent sea-whip) can have high aesthetic values. On the other hand, some quadrats with high species richness and/or high phylogenetic and functional diversity (Fig. 5, triangle) have high ecological values but can show low color heterogeneity (for instance when *Spongia officinalis* the greek bathing sponge, *Codium coralloides* the Crusty codium or *Crisia* sp. a genus of bryozoans are present) and thus are of low aesthetic values.

To map the aesthetic and ecological values of the coralligenous reefs we aggregated information at the station level. In doing so we lost the variance among quadrats within each station but the relatively good fit we found between each metric estimated at the quadrat level and averages at the station level (Appendix H) showed that this strategy was coherent. We mapped each station along the French Mediterranean coastline on a five dimensions map including longitude, latitude, depth, ecological and aesthetic values (Fig. 6). Overall, this map encapsulates most of the information contained in our previous analysis and could help integrate deep marine coralligenous ecosystems into conservation and communication programs. Indeed, the conservation status of a marine habitat according to the European Habitat directive is assessed using indicators, including biodiversity indices, that are sometimes complex and not easily accessible to the citizen. Visualization of synthetic aesthetic and ecological values would be much easier to understand for the decision-makers and the general public. By crossing ecological and aesthetic values, this map could also help decision-makers to locate areas of ecological interest (high ecological value) and areas (with high aesthetic value) where efforts could be made to improve ecological value with potential public support for protection. It could also help managers who, at a glance, could identify the places they can communicate about coupling biodiversity and aesthetics and those where it may be interesting to value less attractive but ecologically important species.

The SEM analysis showed no relationship between depth and aesthetic value but a visual look at our map shows that intermediate depth stations have higher aesthetic values (indeed we found a significant quadratic relationship between aesthetic value and depth, Appendix J). This relationship can be explained by the ecology of coralligenous reef builders who need intermediate levels of light to fully develop (Ballesteros 2006). Note that this nonlinear relationship could not be detected in the SEM analysis which considers only linear relationships. We also found no effect of longitude or latitude on aesthetic or ecological value. However, a visual look at the map clearly shows that on the mainland, the stations close to Marseille have higher aesthetic values (Fig. 6a). When keeping only the stations at the east of Marseille, we found indeed a negative relationship between aesthetic values and longitude (Appendix J). The stations close to Marseille, are located between 30 and 60 m at the intermediate depths where the aesthetic value was the highest (Appendix J: Fig. J.1a). Further eastward mainland stations are distributed on a broader scale of depth: from 22 m for the shallowest to 84 m for the deepest. On the other side, the stations at the west of Marseille, are also of intermediate depths but the influence of the Rhône River plume which brings a lot of sediments and the possible toxic inflows from the Berre lagoon (Kanzari et al., 2012) could explain why they showed lower aesthetic value than stations at the east of Marseille. We also found that when taken apart, the stations in Corsica have a higher aesthetic value than the stations on the mainland. The exceptionally low population density of Corsica (39 inhabitants per km^2 in Corsica; 1019 inhabitants per km^2 for the other regions, (INSEE 2018) might explain this result as the coralligenous reefs are globally less impacted by human activity and thus have higher aesthetic values.

5. Conclusion

Measuring the aesthetic value of biodiversity has become of strong interest given the need to measure non-material benefits provided by ecosystems (Díaz et al., 2018). Due to their relative inaccessibility, marine ecosystems are under-represented in most studies measuring ecological aesthetics of ecosystems (Tribot et al., 2018). But considering the impact of the aesthetic experience in the human collective willingness to conserve natural ecosystems (Gobster et al., 2007; Saunders, 2013), it is essential to evaluate the aesthetic value of these ecosystems too. Here we provide a standardized estimate of aesthetic value of coralligenous reefs using a performant deep learning algorithm based on image analysis. When compared with other biodiversity metrics we showed that a considerable amount of aesthetic value was explained by taxonomic diversity and species composition which indicated a positive relationship between coralligenous diversity and human experience. We also found that human preference was not necessarily linked to ecological values which echoes previous studies that pointed out aesthetic bias in human perception of nature (Graves et al., 2017; Tribot et al., 2019; Dos Santos et al., 2020; Bellwood et al., 2020). Our study also provided among the first maps of the aesthetic value of an emblematic ecosystem at a large scale which will be of strong interest for conservation and restoration programs and communication to the public. Note that, to complete the present work and evaluate completely the aesthetic experience provided by coralligenous ecosystem reefs, the presence of the associated fishes should also be taken into account (*e.g.* Tribot et al., 2019). Overall, our study offers a new, transposable, and quantitative tool that could be of strong interest to evaluate an underestimated facet of ecosystem NCP: the ecosystem aesthetic experience (Tribot et al., 2018a, 2018b); particularly at a much larger scale than what has been done so far. This approach could easily be transposed to other marine ecosystems such as coral reefs but also to terrestrial habitats where images are commonly used as a support to evaluate human preference for natural landscape (*e.g.* Lenormand et al., 2018) but where image analysis using deep learning has not yet been developed.

Open research statement: The code developed for this study and data are available from Zenodo (https://doi.org/10.5281/zenodo.4946778). The photographic material (7692 images) can be provided upon request to Andromède Océanlogie (julie.deter@andromede-ocean.com).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107935.

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