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Community ecology

Species diversity and composition drive the aesthetic value of coral reef fish assemblages

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Cultural and recreational values of biodiversity are considered as important dimensions of nature's contribution to people. Among these values, the aesthetics can be of major importance as the appreciation of beauty is one of the simplest forms of human emotional response. Using an online survey, we disentangled the effects of different facets of biodiversity on aesthetic preferences of coral reef fish assemblages that are among the most emblematic assemblages on Earth. While we found a positive saturating effect of species' richness on human preference, we found a net negative effect of species abundance, no effect of species functional diversity and contrasting effects of species composition depending on species' attractiveness. Our results suggest that the biodiversity–human interest relationship is more complex than has been previously stated. By integrating several scales of organization, our study is a step forward in better evaluating the aesthetic value of biodiversity.

1. Introduction

Understanding the main drivers of the cultural value of biodiversity is an important challenge in biodiversity science [1]. Among cultural ecosystem services, the aesthetic value of biodiversity is central because it contributes to human well-being and cultural experience [2]. The aesthetic value also plays a major role in conservation and management as people are generally more prone to protect what they find beautiful [3–6]. To this end, an increasing number of studies have evaluated the aesthetic value of biodiversity and natural landscapes [7]. While these studies have revealed an overall positive relationship between species' richness and aesthetics, the question of the relative importance of the different scales of biodiversity organization (from individual to communities and ecosystems) to the aesthetic response remains open.

At the individual level, some species can be perceived as more attractive than others, depending on emotional and cultural dimensions (e.g. attraction and fear) [8]. This aesthetic bias has been shown to potentially disconnect human interest from species' ecological uniqueness [9]. At the community and ecosystem levels however, the diversity of functional traits (e.g. body size and shape) among species can contribute positively to human perception by increasing the overall perceived complexity (e.g. [10,11–13]). Other facets of biodiversity such as compositional diversity and species' relative abundances might also come into play in human perception (e.g. [14]). Overall, the human brain combines ecological information into emotional responses, but the relative contribution of these different facets remains to be explored [15].

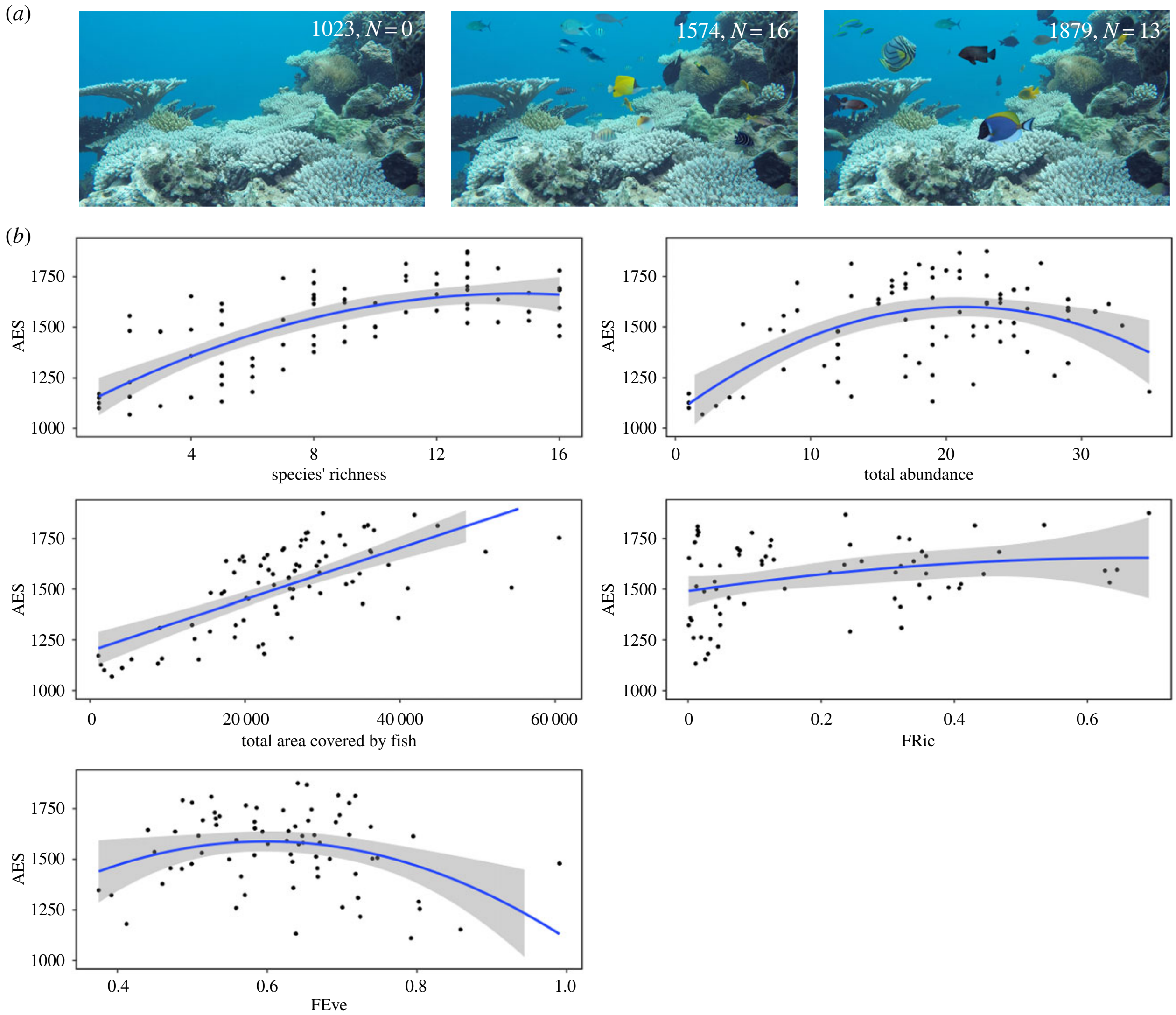

Figure 1. (*a*) Example of photos used in the questionnaire with low, intermediate and high assemblages' aesthetic scores (AES). Species' richness (*N*) is written on each photo. (*b*) Relationship between AES and species' richness, total abundance, total area covered by fish, functional richness (FRic) and functional evenness (FEve) of assemblages. Relationships with 95% confidence intervals are plotted (electronic supplementary material, table S5.1).

The aim of this study is to quantify the relative contribution of the different facets of biodiversity on the aesthetic value to coral fish communities. Coral reefs are among the most important ecosystems on Earth because of their productivity and biodiversity, providing many goods and services to human populations [16,17]. They host up to 8000 fish species, including many colourful species very attractive to the public [18]. Despite their importance, coral reefs are under high levels of threats [19,20], and understanding the drivers of human emotional response to these ecosystems is of strong interest to evaluate their cultural value. Here, we have measured how species' composition (both taxonomic and functional), relative abundances and species' individual aesthetic value were interacting to explain the aesthetic value of coral reef fish assemblages.

2. Methods

(a) Creating the diversity gradient

We extracted 84 photos from a single fringing reef site in Mayotte (electronic supplementary material, 1). All photos had the same background and the same light conditions (examples in figure 1*a*). Photos contained a total of 66 common coral reef fish from the Western Indian Ocean, representing 18 of the 48 most dominant families of coral reef fish (electronic supplementary material, table S2.1). This set of 84 photos was selected in order to create a gradient of fish taxonomic and functional diversity, with 0–16 species and 0–35 individuals (electronic supplementary material, S1 and S3). We refer to photos as species 'assemblages' throughout the rest of the text.

(b) Assemblages' aesthetic scores

Assemblages' aesthetic scores (AES) were assessed using an online anonymous survey available to the general public. The questionnaire consisted of a random sampling with replacement of 20 pairs among the 84 assemblages. For each pair (hereafter 'match'), the participant had to choose the assemblage he/she felt the most beautiful. The assemblages were then scored using the Elo algorithm [21] and the 'EloChoice' R package [22]. Individual aesthetic scores of the fish species found in assemblages were obtained from the previous study (electronic supplementary material, table S2.1 [9]).

(c) Socio-cultural background

Information on socio-cultural backgrounds of the participants was collected during the questionnaire to test the effects of socio-professional factors and experience on aesthetic preferences (electronic supplementary material, S4). We performed an analysis of variance (ANOVA) and tested the effect of each factor on match outcomes.

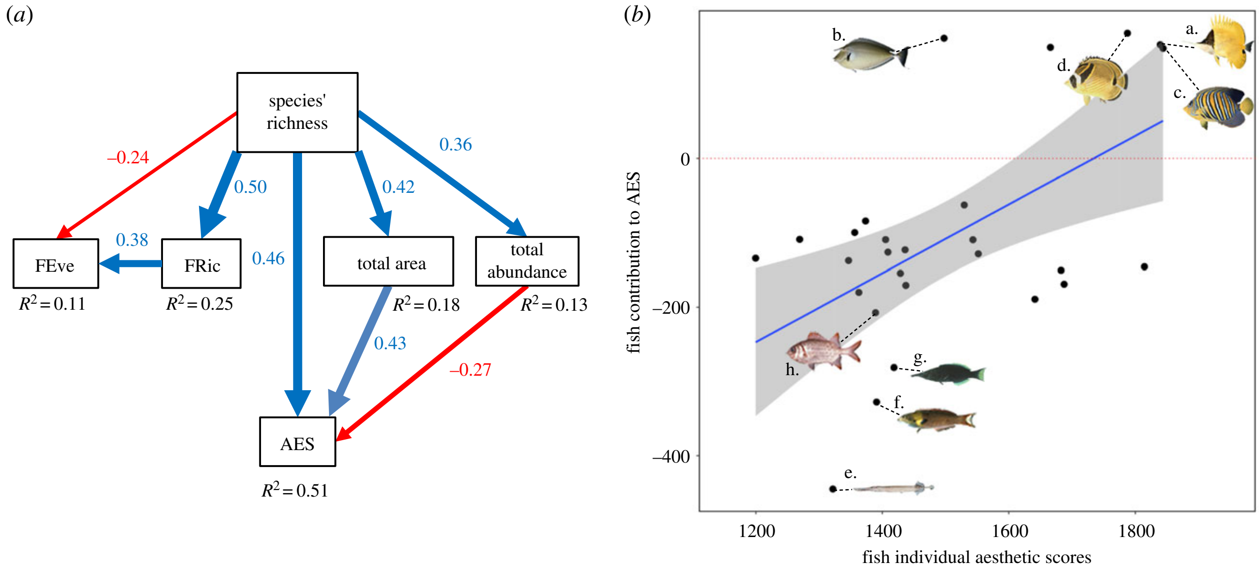

Figure 2. (*a*) Final SEM. Solid arrows indicate significant paths ($p < 0.05$); width of the arrows is proportional to the magnitude of the standardized path coefficient (numbers on arrows); colours indicate the sign of the coefficient (blue for positive and red for negative). R^2 values are shown for dependent variables. (*b*) Relationship between fish species individual AES and the contribution of each fish species to AES (electronic supplementary material, table S5.3). We represent the four species with higher (a. *Forcipiger longirostris*, b. *Naso unicornis*, c. *Pygoplites diacanthus* and d. *Chateodon lunula*) and lower (e. *Aulostolus chinensis*, f. *Thalassoma amblycephalum*, g. *Gomphosus caeruleus* and h. *Myripristis violacea*) contribution to AES. Photographs: J. E. Randall (FishBase.org).

(d) Diversity indices

For each assemblage, different metrics were assessed: (i) species richness was the total number of species, (ii) abundance was the total number of individuals, (iii) the total area covered by fish in each photo was assessed by summing the pixels with fish, and (iv) functional diversity was measured by combining species' functional traits and species' abundances. We used six traits describing fish biology [23]: size, mobility, period of activity, grouping, position in the water column and diet (electronic supplementary material, table S2.2). These traits are linked to the ecology of the fish and to ecosystem processes such as the regulation of food webs and nutrient cycling [24]. A multidimensional functional space was built through a principal coordinates analysis (PCoA) [25]. The three first axes of the PCoA and the species' abundances were used to compute functional richness (FRic), which quantifies the proportion of the functional trait space filled by species and functional evenness (FEve), which quantifies the regularity of abundance in the functional space [26]. Note that FRic cannot be computed with fewer than three species (only 69 assemblages were used for functional diversity analysis).

(e) Effect of diversity on aesthetic preferences

We tested the relationship between AES and the different facets of biodiversity using a set of linear models (including quadratic terms). The normality of the residuals was tested by using a Shapiro–Wilk test. To disentangle the effect of species' richness and other biodiversity facets on the AES, we used structural equation modelling (SEM [27]). The structure of the initial model included direct links between all biodiversity facets and aesthetic scores and between species' richness and other biodiversity facets. Data were centred and scaled, and assemblages with fewer than three species were removed (as FRic cannot be computed with fewer than three species). To account for the nonlinear effect of species richness, we added a latent variable into the SEM in the form of a quadratic species' richness term. The initial SEM model was eventually modified to remove non-significant pathways.

(f) Effect of fish composition on aesthetic preferences

To estimate the individual contribution of each species to AES, we applied a multiple regression approach. Only fish present on more than two assemblages were kept for this analysis ($n = 59$). Multiple regressions were used to examine the variation in AES explained jointly by species' richness and the presence/absence of individual fish species and to rank the individual fish species with respect to the strength of their effect on AES. We first created a linear model (with a Gaussian response) explaining AES given species' richness and fish composition (coded as the presence/absence of each fish species). Species' richness was always entered first in the model, and the presence of individual fish species was ordered in the model according to their independent contribution to the total variation in the response variable. We eliminated non-significant terms using a sequential backwards selection procedure to derive a minimal adequate model. The coefficients of the final model were used to measure the contribution of each fish species to AES. We finally regressed (linear regression) the fish species' individual aesthetic scores against the contribution of each fish species to AES.

3. Results

(a) Assemblages' aesthetic scores

A total of 2137 participants completed the online survey; 90% were 16–60 years old and 60% were women. Managers and engineers were over-represented (45%), as well as 'Ecology' (22%) and 'Biology' (20%) professional sectors. AES ranged from 1023 to 1841 (electronic supplementary material, S3). The ANOVA computed between the outcomes of each match and socio-cultural characteristics did not reveal any significant effect ($p = 0.244$). The scores computed were thus considered robust to the panel of survey participants.

(b) Effect of diversity on aesthetic preferences

Significant relationships were observed between AES and each of the biodiversity facets (figure 1*b*, electronic supplementary material, table S5.1). AES show saturating relationships with species' richness and FRic, hump-shaped relationships with total abundance and FEve, and linear relationship with the total fish area. Total abundance, FRic and total fish area were also positively correlated with species' richness (electronic supplementary material, table S5.2 and figure S6.1). The final SEM model (figure 2*a*, $\chi^2 = 15.187$, d.f. = 10, $p = 0.125$) revealed a positive effect of species' richness on AES, total fish area, FRic and total abundance as well as a negative effect on FEve. Total abundance had a moderate negative effect on AES. Total fish area had a positive effect on AES. The direct FRic and FEve pathways to AES were non-significant and removed from the final model.

(c) Effect of fish composition on aesthetic preferences

The variation in species' richness and fish composition explained most of the variation in AES ($r^2 = 0.94$, $p < 0.001$, electronic supplementary material, S5). Species' richness alone explained 24% of the total variation, whereas species composition alone explains 36% and the variation explained jointly was 30.6% (electronic supplementary material, figure S6.2). The presence of 27 fish species had a significant effect on the AES (electronic supplementary material, table S5.3). The linear model computed between the individual fish species' aesthetic scores and the contribution of each fish species to AES showed a significant positive relationship (figure 2*b*, $r^2 = 0.312$, $p = 0.0024$).

4. Discussion

We show that the aesthetic preferences for reef fish assemblages result from complex interactions between species' richness, species' abundances and composition. Particularly, we found a positive saturating effect of species' richness and a net positive effect of total area covered by fish on aesthetic preferences. When correcting the effect of species' richness on fish abundance and functional richness, we found a net negative effect of abundance and no effect of functional diversity. Previous studies have shown that species functional originality of coral reef fish was weakly involved in aesthetic preferences [9]. Our results scale up this tendency at the level of species assemblages where functional diversity is shown to not influence human interest either. The net negative effect of abundance suggests a negative effect of too much complexity. This finding echoes with studies in environmental psychology that found that environments with intermediate levels of complexity are generally judged as the most beautiful [28,29]. The visual information contained in habitats with high levels of biodiversity would be too difficult to interpret by the human brain, triggering a negative aesthetic response [30]. The non-saturating effect of total fish area suggests that complexity is here better reflected by fish composition and abundance than by the area containing biological information in photos.

Both species' richness and composition were interacting to explain AES. We found a positive relationship between individual species' attractiveness and their contribution to AES. The presence of attractive species could create an immediate positive aesthetic response, leading the observer to make a quick choice without analysing the community as a whole (e.g. [31]). As shown in Tribot *et al.* [9] and Fairchild *et al.* [13], the characteristics that trigger positive responses seem to be bright and contrasted colour patterns (i.e. *Pygoplites diacanthus*). This 'good looking effect' can be related to the 'halo effect' found in human psychology (e.g. [32]) where an unconscious bonus is attributed to physically attractive individuals. However, we also found that less attractive species (i.e. *Aulostolus chinensis*) decrease AES, suggesting that humans integrate both the positive and negative effects of individual fish aesthetic. More robust experimental design (controlling for fish abundances, size and distance from the observer) and the use of an eye tracking system during the questionnaire (i.e. [33]) will be needed before clear connection can be made between fish characteristics, attractiveness and AES but we see our results as a first step toward this goal.

Overall, our study provides experimental evidence that the relationship between diversity and human preference is more complex that previously stated (e.g. [10,11–13]). While all previous studies found a positive effect of diversity on human preferences, we find a saturating effect of species' richness, a net negative effect of species' abundances and no effect of functional diversity. We also show that some species might trigger a negative emotional response. It is likely that the level of ecological complexity at which saturation happens will also depend on the relative size and morphological differences between species and on the phyletic resolution of the assemblages considered (i.e. fish only or fish in association with corals); but still our work is a good illustration of the saturation and bias in human aesthetic judgement. In this study, we used a single background to make the evaluation of fish aesthetic value; thus, future studies will need to test whether the background influences aesthetic perception more than fish biodiversity (e.g. [15]). Note also that we found no effect of the socio-cultural characteristics of observers, suggesting some generality in the aesthetic perception of fish biodiversity. However, more balanced sampling of observers with contrasted socio-cultural profiles and more detailed questionnaires will be needed to confirm this tendency. Understanding the complex nature of humans' emotional response to biodiversity will require more efforts, but we believe that they will contribute to a better evaluation of the human–nature relationship, including aesthetics among other drivers of nature's contributions to people.

Ethics. The online questionnaire and data collection comply with the French Data Protection Act.

Data accessibility. Data are available from the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.931zcrjfm [34].

Authors' contributions. A.-S.T., J.D., T.C., S.V. and N.M. performed the research. A.-S.T. and N.M. contributed equally to analysis and writing. F.G. contributed to analysis. All authors contributed to editing. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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