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Cite this article: Tribot A-S, Deter J, Mouquet N. 2018 Integrating the aesthetic value of landscapes and biological diversity. *Proc. R. Soc. B* **285**: 20180971. http://dx.doi.org/10.1098/rspb.2018.0971

Received: 30 April 2018
Accepted: 14 August 2018

Subject Category:
Ecology

Subject Areas:
ecology

Keywords:
aesthetic value, biodiversity, conservation, ecological functioning, ecosystem services, landscape ecology

Author for correspondence:
Nicolas Mouquet
e-mail: nicolas.mouquet@cnrs.fr

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4205108.

THE ROYAL SOCIETY PUBLISHING

Integrating the aesthetic value of landscapes and biological diversity

Anne-Sophie Tribot[1], Julie Deter[2,3] and Nicolas Mouquet[1]

[1]MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Montpellier, France
[2]ISEM, Univ Montpellier, CNRS, IRD, Montpellier, France
[3]Andromède Océanologie, Carnon, France

NM, 0000-0003-1840-6984

As a cultural ecosystem service, the aesthetic value of landscapes contributes to human well-being, but studies linking biodiversity and ecosystem services generally do not account for this particular service. Therefore, congruence between the aesthetic perception of landscapes, ecological value and biodiversity remains poorly understood. Here, we describe the conceptual background, current methodologies and future challenges of assessing landscape aesthetics and its relationship with biodiversity. We highlight the methodological gaps between the assessment of landscape aesthetics, ecological diversity and functioning. We discuss the challenges associated with connecting landscape aesthetics with ecological value, and the scaling issues in the assessment of human aesthetics perception. To better integrate aesthetic value and ecological components of biodiversity, we propose to combine the study of aesthetics and the understanding of ecological function at both the species and landscape levels. Given the urgent need to engage society in conservation efforts, this approach, based on the combination of the aesthetic experience and the recognition of ecological functioning by the general public, will help change our culture of nature and promote ecologically oriented conservation policies.

1. Introduction

The ecosystem service (ES) framework, while still controversial, has become one of the major instruments for biodiversity and ecosystem management worldwide [1]. Since the Millennium Ecosystem Assessment [2], hundreds of studies have been conducted on the relationship between biodiversity and ESs, mainly focusing on provisioning or regulation [3]. Even if economic values are important, this monetization of biodiversity comes with strong limitations (e.g. [4]) and fails to recognize sociocultural values that are also essential to human well-being [5,6]. To overcome this limitation, the IPBES conceptual framework has defined the concept of Nature's contribution to people (NCP, [7]), which includes both material and non-material links between nature and people such as cultural ecosystem services (CESs). Among CESs, landscape aesthetic value is considered to contribute to quality of life, health or vitality by providing inspiration, harmony and peace [2].

Aesthetic experience is of particular importance as it reflects some of the most intimate links people have with ecological phenomena [8]. It varies according to the scale at which the natural environment is organized and the scale of human perception (figure 1). In return, aesthetic value has potentially a strong influence on people's motivation for biodiversity conservation at both the landscape [11] and species [12] levels. Assessing the aesthetic value of landscapes and identifying its relationship with biodiversity attributes is thus an important issue that should be fully integrated into landscape management and ecological conservation programmes [13].

Aesthetic value can be linked to the physical and ecological properties of landscapes [13], and to management practices [14]. Historically, greater emphasis has been placed on general landscape patterns, mostly structural, in relation

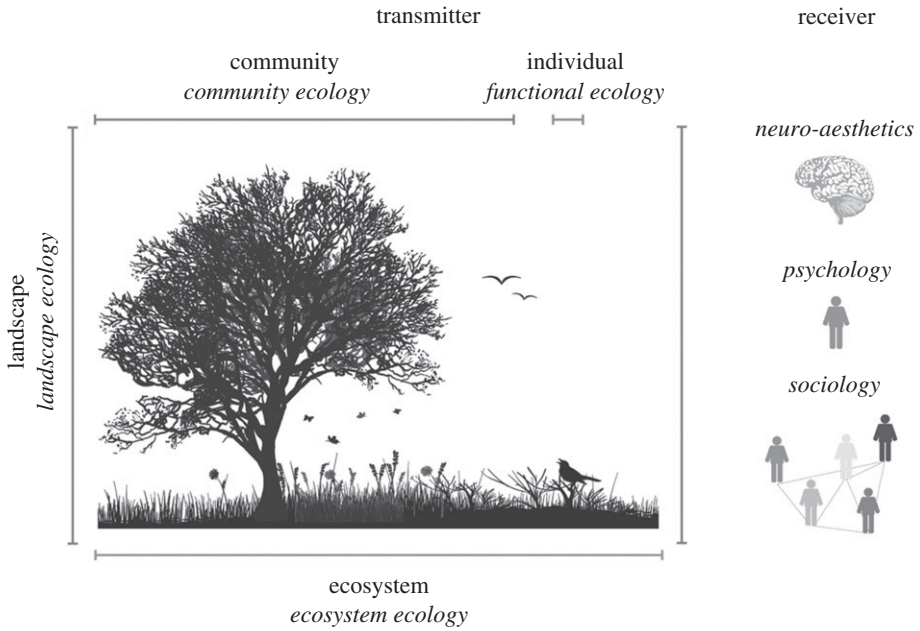

Figure 1. The scales of aesthetic perception. Human perception and aesthetic experience vary according to the organizational levels (from individual to entire landscape) and the level at which humans integrate and share this information. The different organizational scales of the transmitter (i.e. the observed landscape) are studied in different fields of ecological science, from functional ecology, community and ecosystem ecology to landscape ecology. From the receiver point of view, cognitive processes associating visual information to emotion are studied in neuro-aesthetics and psychology. How these emotions are shared within groups concerns the field of sociology. Social science and psychology also study the influence of landscape perception on human behaviours or mental health. Philosophy, art and humanities connect the receiver and the transmitter by studying the relationship between culture and nature (e.g. symbolic values, sense of place [9,10]). Illustrations used in this figure are from vecteezy.com.

to human perception [8,15]. While the relationship between the aesthetic and 'naturalness' of landscapes has been recognized, the definition of naturalness remains vague [16], especially because it is related to human perception and not based on clear biophysical assessment of ecological processes. The concept of 'ecological value', which includes ecological indicators such as biological diversity and ecosystem properties, provides a more operational framework than naturalness [17]. However, the measurement of biodiversity is still missing from the evaluation of landscape aesthetics and is only starting to be considered in the field (e.g. [18–20]).

In the ecological literature, various metrics have been proposed to measure the different facets of biological diversity (taxonomic, functional and phylogenetic), and there is a considerable amount of empirical and experimental evidence of their relationship with ecosystem functioning [21]. Efforts have also been made to integrate ESs into this framework, but mainly by focusing on provisioning and regulating services [3]. This lack of integration of the cultural dimension of biodiversity is clear from the difficulties in finding simple metrics for cultural values [5,22]. To this end, recent developments in the measurement of aesthetic perception of landscapes offer promising opportunities [16] while still lacking explicit measurement of ecological dimensions. The relationship between biodiversity and landscape aesthetics remains thus to be studied within the same framework that has been used to study its relationship with ecosystem functioning and other services [22].

The integration of research programmes aimed at measuring the aesthetic value of landscape and biological diversity can be viewed as a critical step providing metrics of CES operating at the same levels where other ESs (i.e. regulation and provision) are evaluated. Combining aesthetics with biodiversity sciences has the potential to integrate the different scales of ecological organization and human perception into the landscape aesthetics perspective (figure 1) [8]. The aim of this review is to provide a brief description of the main concepts, current methodologies and future challenges of this emerging field. In particular, we (a) highlight the methodological gaps between the assessment of landscape aesthetic value and biological diversity, (b) address the importance of promoting an aesthetic of ecological function based on the recognition of both ecological functioning (i.e. the functions of organisms and ecosystem processes) and aesthetic experience and (c) discuss the relevance of ecological aesthetics for conservation policy.

2. Defining aesthetics

Aesthetics concerns a vast range of disciplines from art and philosophy to social science and cultural history. Aesthetics thus has different and complementary meanings depending on the field in which it is defined. Primarily, aesthetics is a branch of philosophy that questions the beauty in art and aesthetic valuation of artworks [23]. According to psychologists, it is related to the human ability to judge objects from many perspectives, i.e. in terms of emotions, practical use, rarity and experience [24]. When this affective response is positive, it generates pleasure, which can particularly be felt through the observation of *beauty* (defined as the characteristics of the observed object [25]). In classical aesthetic theory, 'beauty' is conceived in terms of harmony, symmetry, order and measure [26]. Aesthetics is here defined by the characteristics of the observed object, i.e. from the perspective of the 'transmitter'. By contrast, Hume [27] suggests that beauty is not an inherent quality of objects but is modulated by education and human nature. Similarly, Kant [28] defines the 'aesthetics of

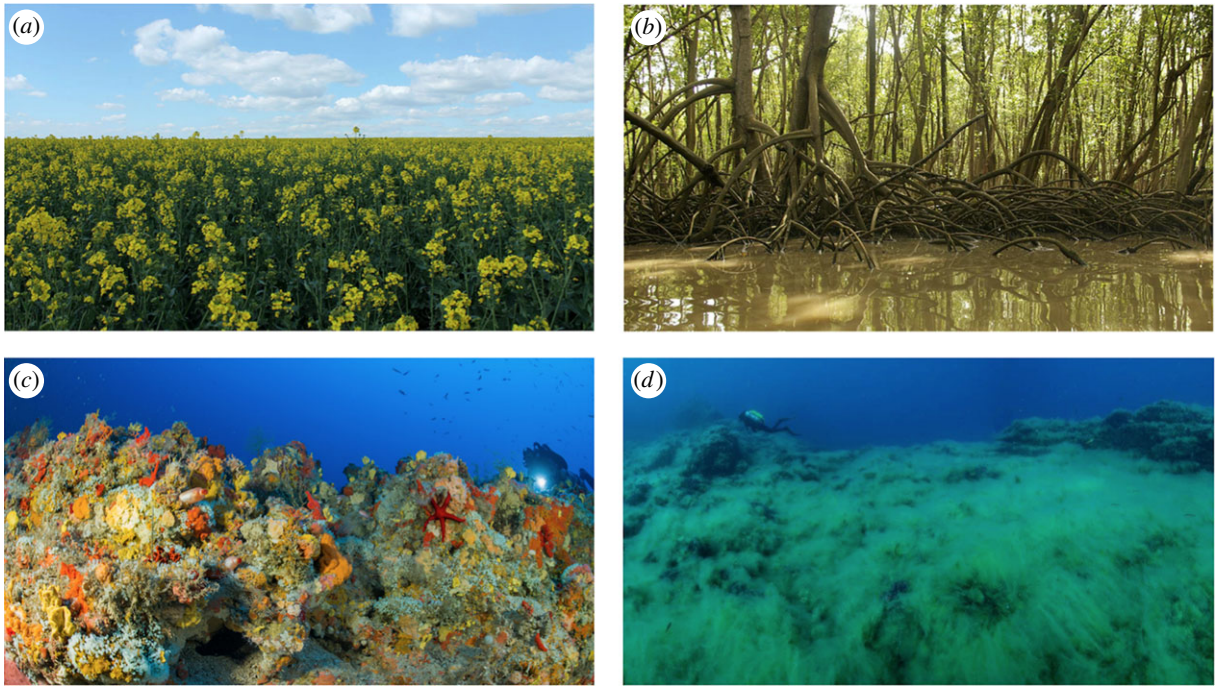

Figure 2. (*a*,*b*) Agricultural versus natural landscapes. Following the processing fluency theory of aesthetic pleasure [30], (*a*) an agricultural landscape, with low biodiversity, can be perceived as aesthetic because of its symmetry, contrasting patches and repeated patterns, but (*b*) a mangrove landscape, with high biodiversity, may be perceived as less aesthetic because of its visual complexity and disorder. (*c*,*d*) Healthy versus degraded ecosystems. (c) A healthy coralligenous reef with high biodiversity might be perceived as more aesthetic than (*d*) a degraded coralligenous reef with lower biodiversity. Photos © (*a*) G. Long, (*b*) J. Housset, ONF Martinique and (*c*,*d*) © L. Ballesta, Andromède Océanologie. (Online version in colour.)

reception', which is a judgement based on subjective feelings. These two views are complementary, interconnected and are the basis of the modern approach that defines aesthetics between the transmitter and the receiver (figure 1). Some views of aesthetics, as in philosophy of arts, consider beauty not as a physical property, but as a relation between an object and an observer, as a bridge between the receiver and the transmitter. Beyond beauty, other views also include social and moral aspects of arts, involving meaning and representations in aesthetic experience [23].

(a) Neuro-aesthetics and evolutionary psychology

Neuro-aesthetics defines the aesthetic properties of objects (transmitters) that lead to the aesthetic experience in the brain of the observer (receiver) [25], and aims to address the nature of aesthetic experience from a science-based perspective, complementarily to classical definitions mentioned above [24]. Ramachandran & Hirstein [29] proposed the 'rules of artistic experience' as a list of aesthetic properties related to neurophysiological mechanisms. The first is the 'peak shift principle' caused by the exaggeration of appreciated features. Another is the 'grouping and binding' linked to the pleasant sensation generated when our brain can group several splotches together or delineates an object from the background. Along this line, the processing fluency theory of aesthetic pleasure [30] integrates these properties in a common framework and links pleasure to the fluency with which information flows through the cognitive system: people prefer objects that they can easily perceive. For example, repeated patterns are considered aesthetic because their predictability increases the speed at which they can be analysed by the brain (figure 2*a*,*b*). In parallel with neuroscience, evolutionary psychology suggests that aesthetic preferences have played a role in human survival [31]. It has been hypothesized that, throughout their evolutionary history, humans have been selected to be extremely proficient at gathering and processing information from their environment; landscape aesthetics being the expression of a preference for simple and reliable information about environmental quality [8,31].

(b) Landscape aesthetics

Landscape aesthetics is defined as the enjoyment and pleasure felt through the observation of environmental scenery [13]. As in philosophy and neuro-aesthetics, it can be divided into two complementary approaches: (i) the transmitter approach, which is linked to the intrinsic value of a landscape as assessed by the biophysical characteristics that stimulate an aesthetic response [16], and (ii) the receiver approach, which describes the landscape through the lens of human perception [5], i.e. the cognitive processes measured by neuro-aesthetics, the psychological interpretation of emotions and the sociological integration of cultural backgrounds (figure 1) [25,32,33]. While aiming at integrating the cultural dimension of natural ecosystems into the ESs framework, most of the approaches developed so far lack operational definitions and metrics to link the aesthetics perception to biological features of natural landscapes [5,17]. They mostly study the receiver dimension, by defining aesthetics through psychological (e.g. tranquility) and cultural (e.g. education) and consider only simple landscape (e.g. presence of water, greenness) properties. The challenge remains to include the ecological attributes of the transmitter (figure 1) by linking the metrics measuring biodiversity and functioning components of landscape with the aesthetics perception.

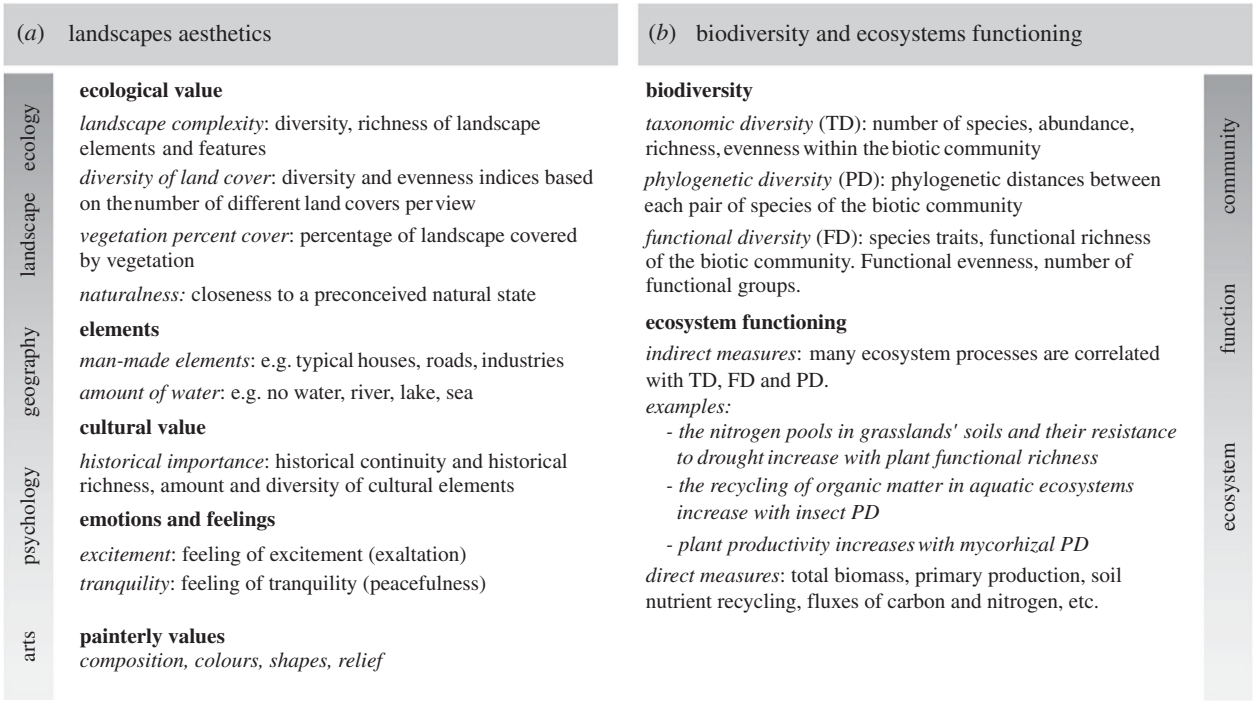

Figure 3. Landscape aesthetics, biodiversity and ecosystem functioning are assessed by distinct scientific fields with different metrics. (*a*) Landscape aesthetics are evaluated either indirectly, by measuring landscape characteristics (in landscape ecology and geography), or directly, by the perception of the observer (in geography and psychology). The first group of metrics are based on mathematical analyses of images, and assign ecological value through landscape complexity, land cover diversity, vegetation cover or naturalness. The presence/absence of particular elements in the landscape, such as the occurrence of water, is also used. The second type of metrics are based on human perception (i.e. cognitive and psychological aspects of aesthetic experience), such as cultural value and emotions, and are generally assessed by photographic surveys. For each metric, the given examples are illustrative and not exhaustive. (*b*) Assessment of biodiversity and ecosystem functioning. Biodiversity is mostly estimated by three complementary measures: (i) taxonomic diversity (species richness), (ii) phylogenetic diversity (evolutionary history of species) and (iii) functional diversity (diversity of morphological, physiological and ecological traits). Ecosystem functioning can be assessed either directly, by measuring ecosystem processes such as primary production or soil nutrient recycling, or indirectly, by using functional and phylogenetic diversity as proxies for the efficiency of ecosystem processes. The different metrics mentioned in this figure are detailed in electronic supplementary material, tables S1 and S2.

3. Linking landscape aesthetics and ecological attributes

(a) What has been done so far?

Some landscape aesthetic studies combine mathematical descriptions of landscapes with human perception metrics, and most of these investigations have found an aesthetic preference for 'healthy' ecosystems with high ecological value [8] (figure 2*c*,*d* for an example). In these studies, measures of ecological value are indirect and estimated by physical metrics, such as the richness and evenness of landscape components (figure 3; electronic supplementary material, table 1). They assume that the landscape structural heterogeneity (electronic supplementary material, table 1) corresponds to high ecological value [34]. For instance, Dramstad *et al*. [35] found significant, positive correlations between aesthetic preference and spatial indicators of landscape structure, such as the number of habitat patches. In landscape ecology, the concept of 'naturalness,' which refers to an 'index describing how close a landscape is to a natural state' [16], is also used, but without a connection to classical metrics of biodiversity and ecosystem functioning. While there are connections between landscape structural metrics of ecological value and biodiversity (e.g. high diversity of landscape elements often correlate with high species richness), explicit measures of biodiversity and ecosystem functioning are almost absent from the landscape aesthetics literature (figure 3). Note also that most (if not all) studies on landscape aesthetics have focused on static visual dimensions; they do not take account of more action-orientated dimensions of perception of landscape such as multisensory perceptions and immersion (e.g. [36]).

Studies linking the aesthetic perception of landscapes, or more generally cultural values such as human well-being or mental health to biodiversity are also emerging [37,38]. However, most of these studies focus on species richness or species abundance only, yet it is now acknowledged that functional traits rather than species number are better predictors of ecological value [39]. Moreover, species richness is not necessarily a significant predictor of aesthetic preference itself because some species are visually difficult to differentiate [40], while people seem to better respond to combinations of functional traits (e.g. colour, shape) [41]. Connecting landscape aesthetics to community ecology and ecosystem functioning thus poses methodological and conceptual challenges that must be addressed to create ecologically oriented landscape aesthetics. In the following sections, we propose possible directions to better assess the links between landscape aesthetics, biodiversity and ecosystem properties.

(b) Quantitative assessments of biodiversity and aesthetics

To become operational, landscape aesthetics needs to produce metrics that can be used in the framework of biodiversity sciences. To do so, biodiversity metrics used in community and ecosystem ecology (figure 3; electronic supplementary

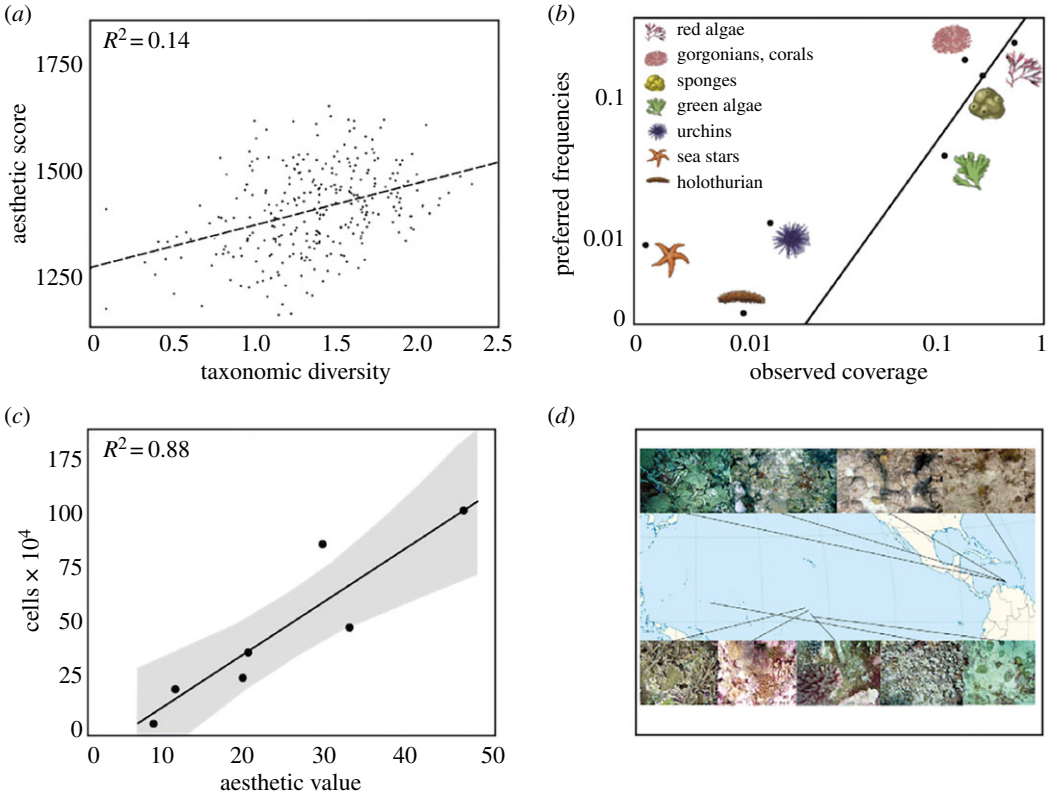

Figure 4. Two examples of direct and indirect relationships between aesthetic value of ecosystems and biodiversity. (*a*,*b*) Direct relationship between aesthetic value and the taxonomic diversity of Mediterranean coralligenous reefs (measured on 338 Mediterranean coralligenous reefs quadrats by 1260 observers during a photo-questionnaire). (*b*) Relationship between observed coverage and preference for different taxa. The vertical axis represents the preferred total frequencies according to observer's declarations (in the questionnaire, each observer had to select the taxon that positively influenced their choice. Frequencies represent the relative number of times that a taxon was chosen), and the horizontal axis represents the observed total coverage of corresponding taxa in photos. The black line (bisector) represents a 'null model' where the preference for a taxon is proportional to its frequency on each photo. Accordingly, gorgonians and corals are the most preferred groups. (*c*) Indirect relationship between aesthetic value (computed using machine-learning algorithms designed to evaluate the aesthetic appearance of art) and the mean bacterial cell abundance (interpreted as a proxy of ecosystem 'health') for (*d*) different coral reefs sampled in the Caribbean and the tropical Pacific. (*a*,*b*) from Tribot *et al*. [19]; (*c*,*d*) from Haas *et al*. [43]. (Online version in colour.)

Table 1. Examples of relationships between aesthetic value and biodiversity.

reference	system studied	biodiversity metrics	methods to assess aesthetic value	relationship
Lindemann-Matthies *et al*. [18]	grasslands	no. of species	photo-questionnaire	+
Lindemann-Matthies *et al*. [42]	gardens	no. of species	photo-questionnaire	+
Haas *et al*. [43]	coral reefs	abundance	computational analysis	+
Cox & Gaston [44]	bird communities	no. of species and abundance	questionnaire	+
Tribot *et al*. [19]	coralligenous reefs	taxonomic, functional and phylogenetic	photo-questionnaire	+
Gunnarsson *et al*. [45]	urban green spaces	qualitative	survey	+
Southon *et al*. [20]	perennial meadows	qualitative	photo-questionnaire	+

material, table 2) should be integrated in the assessment of landscape aesthetics. We do not argue here for the use of only quantitative data to describe aesthetic preferences, which implies some kind of reductionism, but rather to use quantitative assessments as a bridge between landscape aesthetics and biodiversity sciences.

This integration is recent and there are still very few examples of studies linking biodiversity to landscape aesthetics (table 1). Southon *et al*. [20] have shown that plant meadows that contained higher species richness (qualitative measures were used) were preferred most often by green space users. Using more formal indices to measure the different facets of biological diversity (taxonomic, functional and phylogenetic), Tribot *et al*. [19] assessed the relationship between ecological diversity and perceived aesthetics of Mediterranean coralligenous reefs. Aesthetic scores were obtained using online photo-questionnaires and computed with the Elo algorithm [46]. They found a positive relationship between biodiversity metrics and aesthetic values (figure 4*a*) and identified the most preferred taxon (figure 4*b*). The relationship between aesthetics and biodiversity can also be indirect, as shown by Haas *et al*. [43], who

found a significant relationship between the mean aesthetic value of tropical coral reefs and the mean bacterial cell abundance interpreted as a proxy of ecosystem quality (figure 4*c*,*d*). They also found that the most aesthetic reefs were those less impacted by human activity, suggesting a potential relationship between aesthetics and ecosystem health. However, while being informative, most of these studies lack explicit metrics to measure biodiversity or/and landscape aesthetics. We could not find any study linking the ecological components of ecosystem functioning with aesthetic perception.

While quantitative measures of biodiversity can be obtained from biodiversity surveys, quantifying human preference for landscape is more challenging. Methods are heterogeneous, their results are difficult to transpose and they are based on human 'perception'. Estimation of visual preference is among the most common methods used to assess landscape preferences. Photographic surveys are generally used by submitting semantic scales to the observers but such scales are, by definition, qualitative and dependent on the background of the researcher. Providing a quantitative measurement of aesthetic preferences is a real challenge, and one promising direction is to rationalize and randomize the evaluation process. To this end, a large collection of photos can be used, of which a small subset of random pairs can be presented to an observer, who can simply select which he/she prefers. After a large number of photo pairs have been evaluated, an algorithm called 'Elo' [46] can be used to provide a quantitative 'aesthetic score' for each photo [19]. These aesthetic scores can then be correlated to any other ecological or landscape attributes measured at the same spatial scale. Note that using only visual stimulus to measure human perception of landscape restricts aesthetics to the visual, while other aesthetic senses are also very important in our appreciation of nature (e.g. bird song, scent of flowers). For instance, Hedblom *et al*. [47] have shown that the diversity of bird songs had a positive influence on the nature experience of urban landscapes. Integrating these different dimensions of human perception [36] into simple metrics will need to combine quantitative and qualitative measures of nature experience, which remains a real challenge.

(c) Connecting landscape aesthetics with ecological value

Because human perception can incorporate a large amount of information into a single aesthetic judgement, we might potentially evaluate the aesthetic value of entire sites using standardized photos or *in situ* interviews, but this is not true for ecological value. Such an evaluation would need to aggregate data from very different sources, such as species richness, trophic composition, carbon storage and nutrient fluxes (among others). However, these data are rarely available, and the most parsimonious way of evaluating the ecological value of biodiversity remains to evaluate functional diversity (figure 3). The rationale behind the functional approach is that ecosystems are supposed to be healthier (e.g. better productivity, resilience, resistance to invasion, etc.) when the diversity of ecological traits among species is higher [39]. The scale at which functional diversity is measured will depend on the quality of the available data (species traits, distribution of main functional groups, etc.). However, it is not always possible to measure functional traits. Alternatively, using the total phylogenetic distance among visible species in a particular landscape is a promising direction because phylogenetic diversity estimates the functional space of a community and thus, indirectly, ecosystem functioning [48].

(d) Scaling issues in perception assessment

A challenging issue remains also to understand how the human mind integrates information when analysing a landscape (figure 1); are preferences related to a combination of different types of information perceived at a fine scale, or are they resulting from large-scale perception? Additionally, how are biotic components perceived at various levels of organization? Usually, landscape aesthetic studies define the scale at which humans perceive a landscape as the 'perceptible realm', which is the result of a combination of different biotic and abiotic features [8]. Because this 'perceptible realm' is relatively large (an entire landscape), the aesthetic perception of finer scales (e.g. a portion of a landscape or a single species) has remained relatively unexplored, but recent studies have shown that landscape elements, such as species, are important to our perception of nature. For instance, Hula & Flegr [41] found, at the species level, that radially symmetrical flowers with low complexity and sharp contours were preferred, while at the community scale, Cox & Gaston [44] found that urban households preferred to see high bird species richness rather than high number of individuals from the same bird species. Connecting these studies with neuro-aesthetic approaches [25] would aid our understanding of how the human brain processes visual complexity. The way this information is perceived could, for instance, be addressed by using eye-tracking techniques that provide a quantitative way to measure people's observation of landscapes [49]. While promising, the usefulness of this method, to assess landscape ecological perception, still needs to be evaluated (for example by comparing the visual impact of different biological landscape features). Solving these issues will necessitate an exhaustive evaluation of the biotic components of entire landscapes along with a parallel evaluation of human perception at different spatial and ecological scales, which remain to be done.

(e) Linking the transmitter to the receiver

When accurate measures of landscape aesthetics and ecological value (the transmitter) are available, they can be compared with human perception (the receiver) and interpreted in cultural and evolutionary contexts. For instance, a positive correlation between landscape aesthetics and ecological value has been interpreted within an evolutionary framework, which states that humans seek beneficial habitats with ecological features and processes essential to their survival and well-being [31]. Junker & Buchecker [50] found that aesthetic preferences for rivers were highly correlated to their eco-morphological quality, i.e. the structural state of the river as a proxy of ecological quality. The reverse is also true: aesthetic preferences may influence management choices and shape the appearance and ecology of landscapes. For example, visual order is central for French gardeners with direct consequences on the aesthetics and the biodiversity of their gardens [51].

Note that while most of the studies reviewed here have found a positive relationship between aesthetic preference and landscape structure, their results are limited by the semi-natural state of the landscape studied. It is likely that

different results would be expected if more natural landscapes were used, such as mangroves or swamps, that are likely to trigger negative emotional responses when compared with semi-natural and agricultural landscapes (figure 2*a*,*b*). Swamps, for example, present a very high ecological value but also clear risks to humans (i.e. disease agents linked to stagnant waters) and are thus rarely perceived as beautiful. Processes associated with decomposition also provide good examples of the disconnection between human perception and ecological function. Indeed, our aesthetic judgement, which has an evolutionary origin, is mainly driven by short-term survival needs and is not necessarily a function of ecological cycles [52]. For instance, Hagerhall [53] showed that 'well-maintained pastures' (which are not ecological viable ecosystems) were preferred to 'wild nature scenes' because the perception of human influence over a landscape leads to a feeling of safety. Highly designed landscapes, such as urban green spaces, are also expected to show a decoupling between perception and ecological functioning.

Human aesthetic preferences are partially determined by evolutionary processes but are also influenced by the socio-cultural context. Bourassa [32] proposed an integrative model of perception, dealing with biological, cultural and individual dimensions of landscape preference. He pointed out the importance of cultural and individual variability when evaluating landscape aesthetics. For instance, knowledge and experience lead to a better understanding of ecological phenomena, including both living and non-living elements [54], and enhance the aesthetic experience [55]. Müderrisoglu & Gultekin [33] showed that the context in which children grow up had a strong effect on their appreciation of landscapes: children from rural areas preferred rural landscapes, whereas children from urban areas preferred human-built landscapes. Along the same line, Gunnarsson *et al*. [45] found that highly urban-oriented people were giving higher aesthetics scores to urban green spaces than highly nature-oriented persons. Beyond the individual knowledge and experience, the concept of sublime is also important in the environmental experiences by triggering admiration and humility [56]. If we are to integrate the aesthetic value of landscapes into the evaluation of CES, these complex feedback loops between the transmitter and the receiver should also be taken into account.

4. Discussion

(a) Towards an aesthetics of ecological function

Ecological aesthetics aims to explore the relationship between aesthetic and ecological values [8]. It is based on human engagement with the natural environment coupled with an understanding of ecological function [57]. As explained above, a major component of aesthetics is the link between a transmitter approach (a focus on the intrinsic characteristics of objects) and a receiver approach (a focus on objects as perceived by the observer). Neuroscience, psychology, sociology, art and humanities are the lenses through which we can understand this relationship. Linking this understanding to the ecological functioning could, in turn, improve conservation strategies and landscape management. The concept of 'functional beauty,' which can be summarized as 'which can be recognized, used and understood is more appreciated', has been used to explain the aesthetic appreciation of art as well as architecture, design and nature [54]. This concept could be adapted to the ecological perspective by defining an 'aesthetics of ecological function' that would link the aesthetics of landscape perception to the comprehension of ecological functioning. This could be an opportunity for the scientific community to incorporate within the same framework, information on the functioning of ecological systems, and how people perceive them, which is fundamental to the definition of CES and for the educational purpose.

Defining the aesthetics of ecological function requires adequate measures of the relationship between landscape aesthetic perception and ecological value. Furthermore, it opens educational opportunities because aesthetic preferences depend on the experiences, knowledge and uses of landscapes by observers [57]. The effects of experience and education on aesthetic perception have been particularly well studied in arts, where it has been shown that education and experience significantly improve enjoyment during aesthetic experience (e.g. [58]). Although this effect has not yet been fully tested for landscapes, it has been proposed that knowledge shapes the aesthetic judgements of landscapes, in the same way that education influences the appreciation of art [59]. Understanding the functions of the various perceptible elements within an ecosystem may indeed render it more unified to an observer and thus more aesthetic [55]. Education or experience can potentially reinforce or even create this positive relationship [8]. For instance, while our neurological mechanisms (processing fluency) make us less likely to appreciate a mangrove because of the chaotic geometry of the aerial roots (figure 2*b*), integrating the aesthetics of ecological function compels us to appreciate the importance of these roots, which are an adaptation to a low-oxygen environment, and thus enhances our aesthetic perception of this apparently 'messy' landscape [54]. Therefore, linking ecological function and aesthetics has the potential to create a virtuous circle in a collective, conservation-based, aesthetic loop (figure 5). A promising, though indirect, example of the positive feedback between aesthetic value and biodiversity has been described by Hale *et al*. [60], who found that avian species diversity significantly increased in locations that adopted aesthetic landscape planning.

Note that exploring ways in which the public can be educated to aesthetically appreciate natural landscapes through ecological understanding also requires us to understand why the public's aesthetic priorities hold alongside the values scientists have of biodiversity and ecosystem functioning (e.g. [38,61]). This decoupling between ecological understanding and aesthetics can also be found at smaller levels of organization such as species. This is, for example, one of the caveats with zoos, which present a biased representation of nature to the general public [62]. Despite the use of 'beautiful' species by some zoos to intentionally promote conservation programmes [63], it has been shown that their impact on visitor behaviour is low because people spend more time observing animals than learning about them [64]. Similarly, flagship umbrella species are intended to promote public awareness and to raise funds for conservation, as well as provide protection for co-occurring species [65]. However, the usefulness of umbrella species to protect other taxa assemblages is still debated [65,66]. This disconnection has been illustrated by Tribot *et al*. [67] who found that unattractive coral reef fishes have a much higher functional richness than more attractive species, leading to an 'aesthetic bias'. This bias goes beyond

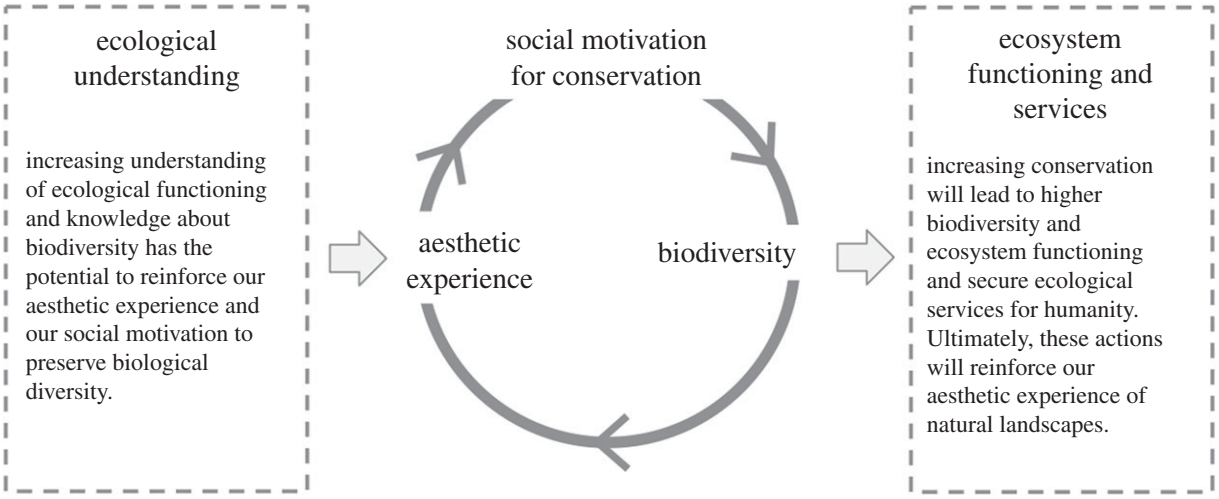

Figure 5. Virtuous loop linking aesthetic value, conservation and biodiversity. Knowledge and experience enhance the aesthetic value of landscapes through the recognition of ecological functioning; landscapes perceived as aesthetic are more likely to be protected; conservation increases the biodiversity of ecosystems, and biodiversity improves ecosystem functioning and services and increases the aesthetic experience, which, fed by knowledge and experience, further increases the social motivation for conservation, etc.

the general public as, for example, researchers publish more studies on birds and mammals than any other taxa [12]. This bias can in turn have strong consequences for conservation biology as, for example, appealing bird species have been shown to have better conservation status [68].

(b) Improving conservation policy

Quantifying the CES provided by biodiversity and measuring the connection between humans and nature is considered a major challenge by the IPBES [1], and we believe that research on landscape aesthetics will help achieve this goal. Once a proper conceptual background is defined and the corresponding methodology is developed, it will be necessary to address the operational dimension: how does the understanding of the connection between landscape aesthetics, ecological value and biodiversity lead to improved conservation policies [69]? As discussed above, understanding the drivers of people's emotional responses to landscape and biodiversity will help develop operational conservation programmes based on a good understanding of human perception of ecosystems. For example, this could help to adapt communication strategies towards the conservation of particular habitat and/or species. Furthermore, understanding the relationship between aesthetic and ecological value will also prevent the drawbacks of human cultural aesthetic bias towards beautiful landscapes and/or species. We found some evidence in the literature of a positive relationship between biodiversity and aesthetic perception (table 1), but there is no *a priori* reason to expect any universal positive relationship between beauty and ecological functioning. As illustrated with coral reef fishes, at the species level, the most beautiful species might even show the lowest functional originality [67]. Many ecosystems (e.g. mangroves, swamps) might indeed show high ecological values and diversity but low or even negative public emotional response; and the inverse is true for ecosystems with low ecological values and diversity but high emotional values (e.g. deserts, rural landscapes).

Incorporating human perception into conservation policy will help in finding the potential synergies and conflicts between human emotional perception and biological conservation priorities and thus identify new policy opportunities. Global assessment of landscape ecological value, including biodiversity, and aesthetic perception remains to be done [7] and we believe it has the potential to be a useful tool for policy-relevant conservation science. Such integration will link conservation research and outcomes to policy processes from the local (e.g. species or habitat conservation programmes) to the global (i.e. IPBES conceptual framework) scales.

5. Conclusion

The relationship between the aesthetic value of landscapes and biodiversity is directly relevant to the general public and could be at the forefront of conservation biology. Understanding its origins will need to combine elements of sociology, psychology, neurology and ecology. We have shown that researches into landscape aesthetics are growing but should be better connected with classical descriptors of community and ecosystem ecology to become fully operational. This integration will need to combine the scales at which humans integrate ecological information and the scales at which landscape components are measured. Human aesthetic perception is a complex behaviour where cultural background plays a central role. Linking our aesthetics with conservation priorities will need to incorporate this complexity and provide elements of education to adapt our perception of nature through the lens of ecosystem functions, including species, communities and ecosystem processes. We believe that addressing together the aesthetic dimension of landscapes with their ecological dimensions will provide the necessary scientific and sociological foundation for this paradigm shift to occur.

Data accessibility. This article has no additional data.

Authors' contributions. A.-S.T., J.D. and N.M. conceived the idea. A.-S.T. and N.M. contributed equally to the writing. J.D. contributed to editing.

Competing interests. We have no competing interests.

Acknowledgements. We thank the Fondation de France and the CNRS for funding. We also thank L. Ballesta, G. Long and J. Housset for providing photographic support, as well as A. Haas for providing figure 4*c*,*d*. We are grateful to C.N. Meynard, S. Villéger and J. Renoult for comments on an earlier version of the manuscript.

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