

RESEARCH ARTICLE

Quantitative Colour Pattern Analysis (QCPA): A comprehensive framework for the analysis of colour patterns in nature

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Abstract

1. To understand the function of colour signals in nature, we require robust quantitative analytical frameworks to enable us to estimate how animal and plant colour patterns appear against their natural background as viewed by ecologically relevant species. Due to the quantitative limitations of existing methods, colour and pattern are rarely analysed in conjunction with one another, despite a large body of literature and decades of research on the importance of spatio-chromatic colour pattern analyses. Furthermore, key physiological limitations of animal visual systems such as spatial acuity, spectral sensitivities, photoreceptor abundances and receptor noise levels are rarely considered together in colour pattern analyses.
2. Here, we present a novel analytical framework, called the Quantitative Colour Pattern Analysis (QCPA). We have overcome many quantitative and qualitative limitations of existing colour pattern analyses by combining calibrated digital photography and visual modelling. We have integrated and updated existing spatio-chromatic colour pattern analyses, including adjacency, visual contrast and boundary strength analysis, to be implemented using calibrated digital photography through the Multispectral Image Analysis and Calibration (MICA) Toolbox.
3. This combination of calibrated photography and spatio-chromatic colour pattern analyses is enabled by the inclusion of psychophysical colour and luminance discrimination thresholds for image segmentation, which we call 'Receptor Noise Limited Clustering', used here for the first time. Furthermore, QCPA provides a novel psycho-physiological approach to the modelling of spatial acuity using convolution in the spatial or frequency domains, followed by 'Receptor Noise Limited Ranked Filtering' to eliminate intermediate edge artefacts and recover sharp boundaries following smoothing. We also present a new type of colour pattern analysis, the 'local edge intensity analysis' as well as a range of novel psycho-physiological approaches to the visualization of spatio-chromatic data.
4. QCPA combines novel and existing pattern analysis frameworks into what we hope is a unified, free and open source toolbox and introduces a range of novel analytical

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and data-visualization approaches. These analyses and tools have been seamlessly integrated into the MICA toolbox providing a dynamic and user-friendly workflow.

KEYWORDS

animal colouration, colour pattern analysis, colour perception, colour space, image analysis, receptor noise limited model, visual modelling

1 | INTRODUCTION

Animal colour patterns are complex traits which serve a multitude of purposes, including defence against predators (such as camouflage and aposematism), social signalling and thermoregulation (Cott, 1940). How colour patterns are perceived by animals is unique to a given visual system in a specific context. It depends on the visual background against which they are viewed, the visual capabilities of the signal receiver, the distance from which the pattern is viewed and the ambient light environment (Cuthill et al., 2017; Endler, 1978, 1990; Lythgoe, 1979; Merilaita, Lyytinen, & Mappes, 2001). Animal visual systems are diverse, and vary in eye shape and size, visual pigment number and absorbance maxima, photoreceptor type and number, and retinal and post-retinal processing (Cronin, Johnsen, Marshall, & Warrant, 2014; Lythgoe, 1979). When determining the perception of colour patterns in other animals, it is therefore essential to consider spatial acuity (and viewing distance) as well as colour and luminance discrimination abilities (Endler, 1978). Humans have greater spatial acuity and contrast sensitivity than most vertebrates, except for some birds (Caves, Frank, & Johnsen, 2016; da Silva Souza, Gomes, & Silveira, 2011). We also have a different number of receptor classes, and different spectral sensitivity ranges compared to many animals (Cronin et al., 2014). For example, most other mammals are dichromats (i.e. they have only 2 compared to our 3 cone types), while most birds, reptiles and some amphibians, spiders and fish possess an ultraviolet cone sensitivity and are probably tetrachromats (Cronin & Bok, 2016; Osorio & Vorobyev, 2005, 2008). Among invertebrates, the number of receptor classes may exceed 10 (Cronin et al., 2014).

To examine the perception of visual signals by animals, studies generally measure colour, luminance and pattern characteristics (e.g. Allen & Higham, 2013; Cortesi & Cheney, 2010; Marshall, Vorobyev, & Siebeck, 2006; Xiao & Cuthill, 2016; Zylinski, How, Osorio, Hanlon, & Marshall, 2011). For example, colour (chromatic) and luminance (achromatic) contrast is measured between colour patches within an animal, or between an animal and its background, and is calculated in terms of perceptual distances in colour space often using the Receptor Noise Limited Model (RNL) (Vorobyev & Osorio, 1998). This model assumes that the noise inside a given class of photoreceptors, in combination with their relative abundance and opponent colour processing mechanisms, are the fundamental limits of colour and luminance contrast perception. The relative stimulation of photoreceptors can then be used to map the perceptual distances between colour patches in colour space (reviewed by Renoult, Kelber, & Schaefer, 2017). These Euclidean, or

geometric distances, are expressed in terms of ΔS values (Siddiqi, Cronin, Loew, Vorobyev, & Summers, 2004; Vorobyev, Brandt, Peitsch, Laughlin, & Menzel, 2001). The model predicts that a 'Just Noticeable Difference' (JND) should be equivalent to $\Delta S = 1$ if model conditions and assumptions are met (Vorobyev & Osorio, 1998). For quantifying the spatial properties of patterns, Fast Fourier Transform (FFT) analyses of pixel intensity in digital images (Switkes, Mayer, & Sloan, 1978), pixel or location dependent transition matrices (Endler, 2012) or landmark based pattern metrics are often used (Lowe, 1999; Troscianko, Skelhorn, & Stevens, 2017; Van Belleghem et al., 2018).

These types of analyses aim to computationally reproduce the retinal processing of visual information, but often investigate colour, luminance or pattern contrast in isolation. For example, Cheney et al. (2014) quantified the conspicuousness of nudibranch molluscs (marine gastropods) by measuring pattern contrast against their natural backgrounds using FFT on digital images. They then measured chromatic contrast (ΔS) between animal and background using point measurements obtained by a spectrophotometer. While useful for many studies of animal colouration, these individual analyses ignore the interaction of visual information at various perceptual stages (for discussion see Endler & Mappes, 2017; Ng, Garcia, & Dyer, 2018; Rowe, 2013; Ruxton, Allen, Sherratt, & Speed, 2018; Stevens & Merilaita, 2011). However, recent publications continue to highlight the need to use an integrated approach to consider visual information when investigating the perception, and therefore the design, function and evolution, of complex visual signals (Dalziel & Welbergen, 2016; Endler, 1978, 1984, 2012; Endler, Cole, & Kranz, 2018; Endler & Mappes, 2017; Hebets & Papaj, 2005; Osorio, Smith, Vorobyev, & Buchanan-Smith, 2004; Rowe, 1999, 2013; Rowe & Guilford, 1999; Ruxton et al., 2018; Shapley & Hawken, 2011; Stevens & Merilaita, 2011). For example, not only is the efficiency of visual signals dependent on the presence or absence of colours, but also how those colours are arranged in patterns (e.g. Endler & Houde, 1995; Green, Urquhart, van den Berg, Marshall, & Cheney, 2018; Sibeaux, Cole, & Endler, 2019, 2019; Troscianko et al., 2017).

Existing methods for spatio-chromatic colour pattern analysis (Endler, 2012; Endler et al., 2018; Endler & Mielke, 2005), which have recently been implemented by PAVO 2 (Maia, Gruson, Endler, & White, 2019), parameterize geometric or chromatic properties of colour patterns such as geometric complexity, regularity, hue and saturation. They also provide parameters which themselves are simultaneously shaped by both spatial and chromatic properties of a colour pattern, such as abundance weighted chromatic contrast measures. However, such analyses require segmented images, meaning images

in which the individual colour patches are delineated. Therefore, they are only suitable for processing colour patterns and visual scenes which have very clear colour differences (sharp boundaries with high chromatic and/or achromatic contrast), so that spectral data can be collected easily from each colour patch. Alternatively, these methods would require a prohibitively large number of spectral measurements to be made from a scene containing typical levels of natural variation; even the lowest acuity receivers would require many thousands of points to be measured. Digital imaging is therefore ideally suited to this type of analysis, because each image can rapidly and non-invasively capture millions of point samples which can provide the necessary chromatic and spatial information. However, currently available image segmentation and processing techniques do not incorporate physiological and cognitive limitations of ecologically relevant viewers. Indeed, many approaches rely on manually drawing the outlines of colour pattern elements by a human observer or clustering algorithms using uninterpreted RGB information inside a digital image (Endler & Houde, 1995; Isaac & Gregory, 2013; Winters et al., 2017). Such approaches inevitably introduce some degree of anthropocentric (qualitative) as well as quantitative bias in interpreting animal colouration, unless the colours fall in clear classes and they have been checked and calibrated with a spectrometer or calibrated digital photography.

In this paper, we introduce a method to overcome these problems and present a user-friendly, open-source framework, which we call 'Quantitative Colour Pattern Analysis' (QCPA). QCPA is a comprehensive approach to the study of the design and function of colour patterns in nature. It combines calibrated digital photography (Stevens, Parraga, Cuthill, Partridge, & Troscianko, 2007), visual modelling and colour pattern analysis into an analytical framework that is seamlessly integrated into the 'Multispectral Image Calibration and Analysis Toolbox' (MICA) (Troscianko & Stevens, 2015). QCPA enables the use of existing, revised and newly developed colour pattern analyses on an unprecedented quantitative and qualitative scale. This is enabled by image segmentation using combined colour and luminance discrimination thresholds (RNL clustering) or naïve Bayes clustering (Supplemental Material) as well as improved modelling of visual acuity (RNL ranked filtering). Pattern analyses included in QCPA are colour adjacency analysis, visual contrast analysis and boundary strength analysis (Endler, 2012; Endler et al., 2018; Endler & Mielke, 2005), which we have expanded, adapted and revised. For example, we introduce local edge intensity analysis (LEIA), an extension to boundary strength analysis (Endler et al., 2018), which allows for colour pattern edge intensity analysis approximating the scale of receptive fields (Cronin et al., 2014; Marr & Hildreth, 1980) of a visual system while not requiring a segmented image. QCPA provides the user with a freely adjustable network of image processing tools which can convert visual information into a highly descriptive array of numbers and representative figures which may be used to examine a variety of evolutionary, behavioural and ecological questions (Figure 1). Potential applications of QCPA include (but are not limited to): background matching, disruptive colouration, polymorphism, mimicry, aposematism, sexual signalling, territorial signalling, thermoregulation and landscape analysis.

2 | MATERIALS AND METHODS

We first provide a brief description of the acquisition of calibrated digital images and theoretical visual modelling of the viewer and then describe individual tools of the QCPA in more detail, including:

- **Modelling of spatial acuity:** using an adaptation of Fast Fourier transform or Gaussian filters;
- **Image smoothing and edge reconstruction:** using the receptor noise limited ranked filter;
- **Image segmentation:** using receptor noise limited clustering and naïve Bayes clustering;
- **Pattern analysis:** using adjacency, boundary strength, visual contrast analysis, local edge intensity analysis and particle analysis;
- **Data visualization:** using ΔS edge intensity images, XYZ chromaticity images, RNL saturation images and colour maps in RNL chromaticity space.

Finally, we describe how the rich numerical output of QCPA can be used to investigate the design, function and evolution of colour patterns in nature. We also provide extensive additional technical details, a glossary and worked examples in the Supplemental Material.

2.1 | Step 1: Acquisition of calibrated digital images

Acquiring data suitable for analysing the spatio-chromatic properties of a scene is the first requirement for implementing QCPA. The open-source and user-friendly MICA toolbox can be used to generate calibrated multispectral images and cone-catch images from almost any digital camera (Troscianko & Stevens, 2015). Cone-catch images model the photoreceptor stimulation of an animal for every pixel within an image, with additional support for ultraviolet (UV)-sensitive cameras when modelling the vision of species with UV sensitivity (Figures 1 and 2) (Troscianko & Stevens, 2015). While hyperspectral cameras are, theoretically, also well-suited to this task (e.g. Long & Sweet, 2006; Russell & Dierssen, 2015), there are a number of limitations in their use including cost and image resolution. However, the QCPA framework can also be used for the analysis of hyperspectral images. Precise instructions on how to obtain high quality calibrated image data are outlined in Troscianko and Stevens (2015).

The MICA toolbox provides its own growing set of image analysis tools (e.g. Troscianko et al., 2017) to which QCPA contributes. Importantly, MICA allows the user to model cone captures in response to any possible light environment. This is very useful as it allows one to observe visual scenes in one light environment (e.g. a flower in a field at noon on a cloudy day) and translate them to another light environment (e.g. the same flower but under a long-wave-length enriched clear-sky sunrise light spectrum). MICA also lets the user switch between spectral sensitivities and cone channels of different species if that information is available (e.g. the same flower observed by a bee in comparison to a bird). This function is increasingly used by a range of researchers to introduce animal colour vision

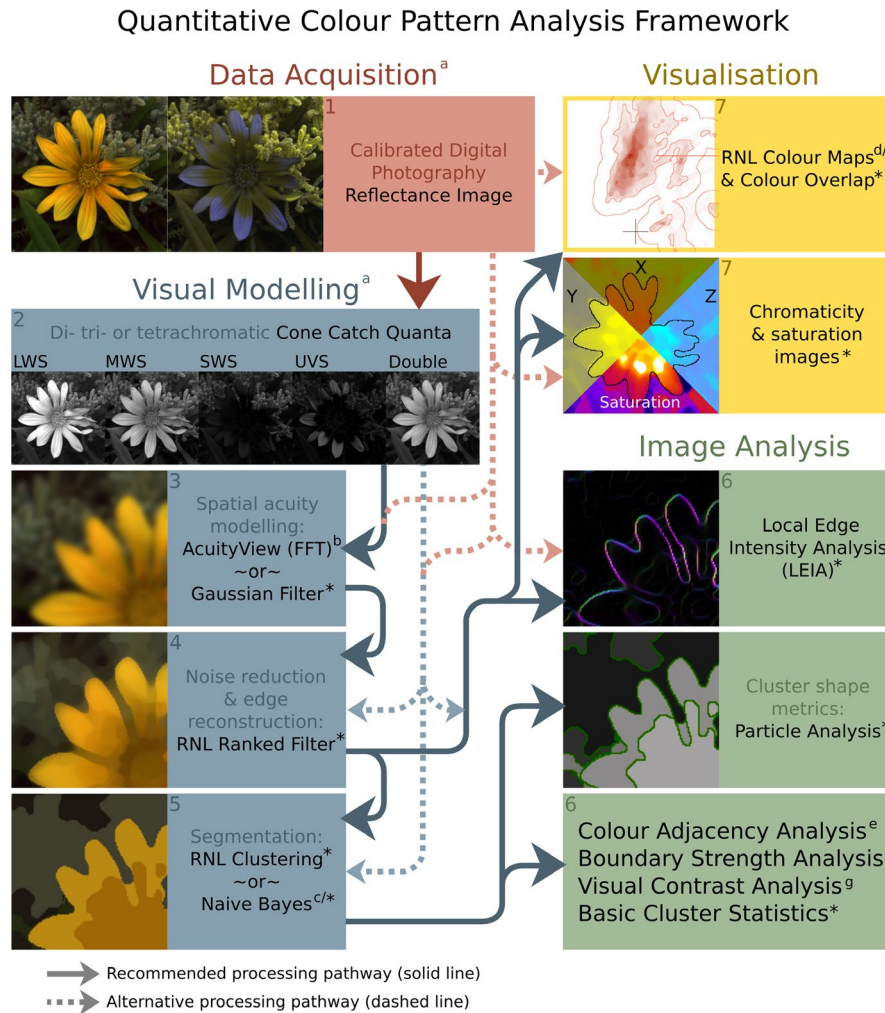


FIGURE 1 Schematic of the ‘Quantitative Colour Pattern Analysis’ QCPA framework. Asterisks (*) show steps in the framework which are novel or have been heavily adapted for use in this framework, while super-script letters refer to existing techniques. Cone-catch images are the input into the framework, which can be generated with the MICA toolbox (^aTroscianko & Stevens, 2015). Spatial acuity modelling is then used to remove visual information which would not be visible given the acuity and viewing distance (using either AcuityView 2.0, ^bCaves & Johnsen, 2017, or a Gaussian convolution-based approach*). Acuity correction generates blurred images with intermediate colours that are not likely to be perceived by the receiver. The RNL ranked filter* is therefore used to recreate sharp boundaries. These images are an ideal input for the LEIA*, and for generating colour maps in RNL chromaticity space (^dHempel De Ibarra et al., 2001; Kelber et al., 2003; Renoult et al., 2017). RNL clustering* or Naive Bayes clustering (^cKoleček et al., 2019) are then used to segment the image prior to colour adjacency analysis (^eEndler, 2012), boundary strength analysis (^fEndler et al., 2018), visual contrast analysis (^gEndler, 1991; Endler & Mielke, 2005) and particle shape analysis*. Numbers (1–7) correspond to the steps listed in section 2

to their colour pattern studies (e.g. Chan, Chang, Huang, & Todd, 2019). Species-specific information on spectral sensitivities is often hard to obtain. However, in many cases, it is possible to overcome this by estimating spectral sensitivities using information from closely-related species (Kemp et al., 2015; Olsson, Lind, & Kelber, 2018).

2.2 | Step 2: Defining discrimination thresholds

The chromatic (ΔS_C) and achromatic contrast (ΔS_L) within an image can be calculated as perceptual distance between any two pixels in 1 to n -dimensional colour space (Clark, Santer, & Brebner, 2017) using the RNL model (Vorobyev & Osorio, 1998) (as per Hempel de Ibarra, Giurfa, & Vorobyev, 2001 for chromatic contrast, and

Siddiqi et al., 2004 for achromatic contrast). In its current state, QCPA uses the RNL equations for bright light (photopic) conditions (see discussion section of this paper for variations of the RNL). These contrasts can then be used to remove pixel noise (fluctuations in pixel intensity due to noise in the camera sensor) from a digital image, as well as for its segmentation into colour patterns. Species specific data on visual systems (particularly receptor noise) can be difficult to obtain (but see Olsson, Lind, & Kelber, 2015). This often results in model parameters being estimated. In combination with deviations from assumptions of the RNL model (Vorobyev & Osorio, 1998) this emphasizes the need to validate discrimination thresholds and model parameter choices using behavioural experiments or choosing conservative thresholds (Olsson et al., 2018).

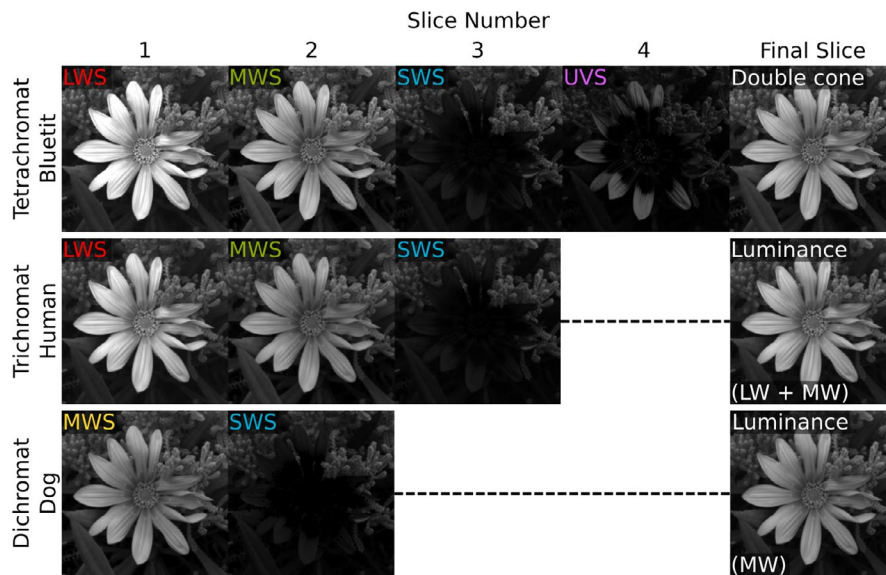


FIGURE 2 Example of multispectral image stacks as an output of Multispectral Image Analysis and Calibration. Note that each image stack has a designated luminance channel layer needed for Quantitative Colour Pattern Analysis to allow inferences based on luminance discrimination thresholds

QCPA tools using the RNL model should be used with caution for animals that may lack colour opponent processing (Toehn, How, Chiou, & Marshall, 2014) or opponent processing that potentially differs substantially from RNL model assumptions (e.g. Rocha, Saito, Silveira, De Souza, & Ventura, 2008). However, QCPA provides alternative image segmentation tools and pattern statistics particularly designed for these instances (Supplemental Material).

2.3 | Step 3: Modelling of spatial acuity

The ability of an animal to resolve patterns depends on the spatial acuity of its vision, which may be determined through anatomical, behavioural or physiological measurements (Champ, Wallis, Vorobyev, Siebeck, & Marshall, 2014), in addition to the distance at which objects are viewed. To understand why animals display particular colour patterns, it is important to investigate if a colour pattern element is visible to an animal from a certain distance (Endler, 1978; Marshall, 2000). For example, a worker bee does not perceive the intricate UV patterns of a flower that guide the bee to its nectar storage until it is close due to the limitations of its visual acuity (Figure 3). QCPA adapts and expands upon existing tools for modelling spatial acuity by using an adaptation of AcuityView (Caves & Johnsen, 2017) and Gaussian filter mediated blurring.

2.4 | Step 4: Eliminating problems in acuity-related processing using the RNL Ranked Filter

As noted by Caves and Johnsen (2017), the blurring of images to model visual acuity (Step 3) is not intended to manipulate images to represent how the scene would be perceived by the receiver; instead, it eliminates details which the specific visual system cannot resolve (Caves & Johnsen, 2017). It is likely that many animals perceive clearly delineated spatial information as the available visual

information is integrated in retinal or post-retinal processing. Blurred edges are also problematic for clustering techniques or boundary comparison techniques and may create artefacts of processing that are likely irrelevant to the animal. Pixel noise fluctuation in the sensor of a digital camera can also interfere with the clustering process, creating false edges, artificial colour pattern elements or influencing edge structure of colour pattern elements.

To overcome these issues, we have developed a filter that can be applied to an image prior to clustering, which we call the 'RNL Ranked Filter'. The filter resembles the 'Smart Blur' used in photo editing software (such as the 'Adobe Creative Cloud') and other rank selection filters, which rank the pixels in a kernel and modify them based on that ranking. However, our custom written algorithm uses an estimate of an animal's psychophysical ability (Using the RNL model) to discriminate between colours and luminance to recreate sharp edges and reduce pixel noise in a cone catch image (Figure 4c, Supplemental Material). While the RNL ranked filter provides a possible solution to reconstruct sharp edges, the extent to which it reflects the perception of spatial information in a given species should be validated with behavioural experimentation.

2.5 | Step 5: Psychophysical image segmentation using RNL Clustering

A range of pattern analyses, including granularity analysis (Stoddard & Stevens, 2010) or NaturePatternMatch (Stoddard, Kilner, & Town, 2014) can be applied to an unsegmented picture (Steps 1–4). Other pattern analyses, such as Patternize (Van Belleghem et al., 2018) or most analyses in QCPA require an image segmented into colour pattern elements. However, image segmentation is often created subjectively using human perception; for example, a researcher estimating how many colour elements there are within a pattern. This may be sufficient for simple patterns but is likely to introduce significant anthropocentric bias when analysing complex patterns and when the visual system of the animal

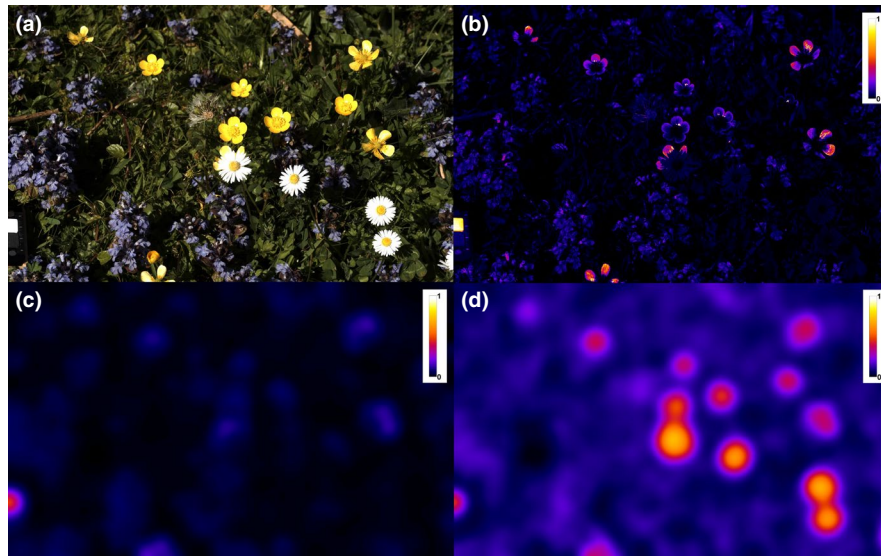


FIGURE 3 (a) A flower meadow as seen by a human observer. (b) UV intensity as detected by a worker bee with superior spatial acuity, which may lead to the false assumption of the UV information being available to the bee from a distance. (c) UV intensity as detected by a worker bee with a spatial acuity of 0.5 cycles/degree at 1 m distance. (d) Medium-wavelength-sensitive photoreceptor stimulation (used for luminance detection) of a worker bee at 1 m distance. Note that the white standard (bottom left) remains detectable in all pictures. The scale in the top right of each image shows the relative stimulation of the given receptor channel. Note that the UV signal contributes to the perception of chromaticity as part of a colour opponency channel in the bee's visual system and is not interpreted individually

differs dramatically from a human visual system. Here, we present an agglomerative hierarchical clustering approach (Day & Edelsbrunner, 1984) which uses colour and luminance discrimination thresholds of an animal, either in combination with each other or separately. By comparing each pixel to its neighbours, we can use the log-transformed RNL model to determine whether any two pixels could be discriminated based on colour and/or luminance contrast perceived by an animal. Once completed across an entire sample, this process results in an image that is segmented according to an animal's psychophysiological discrimination thresholds (Figure 4d). This approach shares similarities with image segmentation techniques in computer vision such as statistical region merging (Nock & Nielsen, 2004). Given the variability in previous investigations examining the relationship between the perception of spatial, chromatic and achromatic information (e.g. Clery et al., 2013; Miquilini et al., 2017; Shapley & Hawken, 2011; Shevell & Kingdom, 2008), we recommend such combined thresholds be confirmed using contextualized behavioural experiments. For more information on the mechanism of the RNL clustering as well as the combination and weighting of chromatic and achromatic thresholds see the Supplemental Material.

2.6 | Step 6: Colour pattern analysis

At this point of the QCPA workflow (Figure 1), the user has an image which has been filtered and modified according to the physiological and psychophysical limitations of an animal visual system, in the context of the physical environment. We can now quantify this information to investigate questions on the design and function of a colour pattern.

In this section, we present a range of secondary image statistics that can be derived from un-clustered (not using the RNL clustering

or alternative image segmentation), filtered (using the RNL Rank Filter) as well as clustered images. We have, for this purpose, adapted and interpreted analytical frameworks such as colour adjacency analysis (Endler, 2012), visual contrast analysis (Endler, 1991; Endler & Mielke, 2005) and boundary strength analysis (Endler et al., 2018). We also present new parameters and alternative outputs of these frameworks, new types of pattern analysis as well as various ways of visualizing and plotting image and pattern properties (Figure 1).

2.6.1 | Colour adjacency analysis

Colour adjacency analysis (CAA) provides an approach for measuring the geometric properties of colour patterns and entire visual scenes (Endler, 2012). The concept is based on measuring the frequencies of transitions along transects across an image parallel and perpendicular to an animal's body axis. The information is captured in a transition matrix which can then be used to derive pattern parameters relative to pattern geometry and potential function. While comparably novel to visual ecology, the use of transition matrices for the quantification of patterns and their emerging properties is well established in landscape ecology (McGarigal & Marks, 1994; Wickham, Riitters, O'Neill, Jones, & Wade, 1996). In addition to providing frequently used metrics describing pattern geometry (e.g. aspect ratio and patch size), CAA enables the quantification of the specific spatial arrangement (adjacency) of colour pattern elements (Figure 5).

Colour adjacency analysis can be used for (but is not limited to) the quantification of mimicry and colour pattern polymorphism, aposematism, camouflage, sexual signalling and studies on evolutionary genetics and evolutionary development of colour patterns (see Endler,

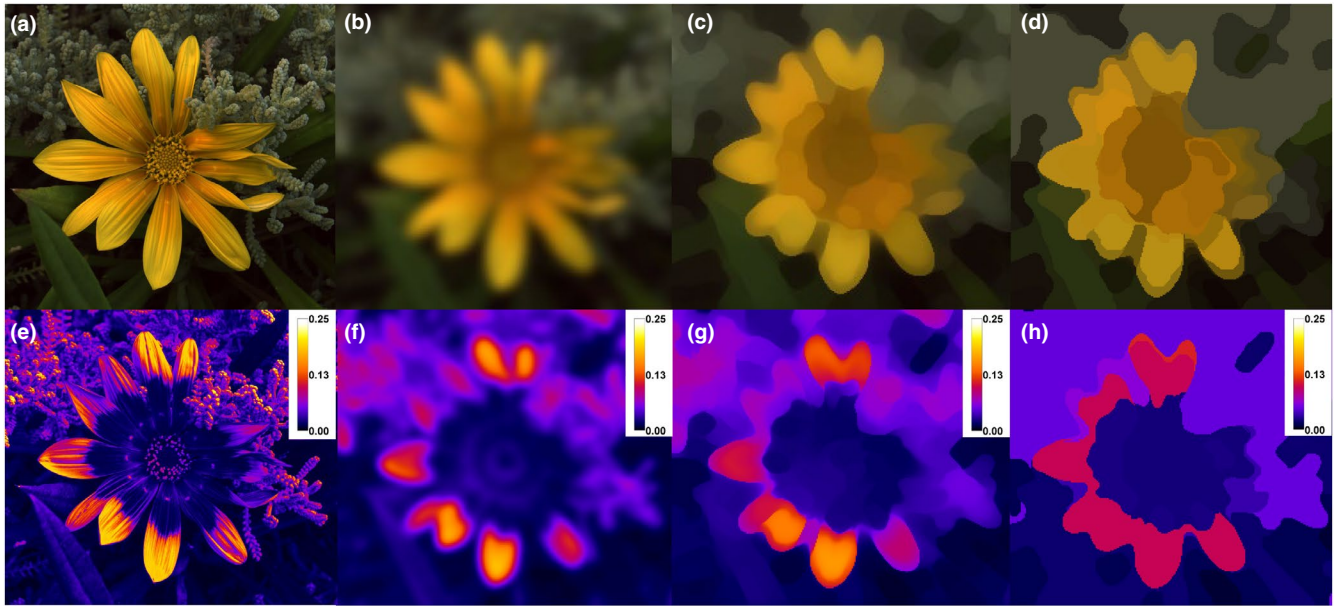


FIGURE 4 (a) Reconstructed RGB image of a daisy using cone stimulation of the short, medium and long-wavelength sensitive photoreceptor channels of a blue tit *Cyanistes caeruleus*. The UV photoreceptor is not shown for simplicity. (b) The image after Fast Fourier Transform filtering using a spatial acuity of 4.8 cycles/degree and a viewing distance of 2 m. (c) Recreation of sharp edges using RNL ranked filtering. (d) Clustering the image into colour pattern elements with Receptor Noise Limited Model (RNL) clustering. (c) and (d) assume a conservative cone receptor noise of 0.05 and a cone ratio of 1:2:3:3 (Hart, Partridge, Cuthill, & Bennett, 2000). Clustering using a colour discrimination threshold of 3 ΔS and a luminance discrimination threshold of 4 ΔS . See Step 1 (Figure 1) for details on multispectral imaging. (e) UV information without acuity modelling as perceived by a worker bee *Apis mellifera*. (f) Acuity modelled at 15 cm viewing distance and 0.5 cycles/degree. (g) RNL ranked filtered as per 15 cm viewing distance and receptor noise of 0.13 (Vorobyev & Osorio, 1998). (h) RNL clustered UV layer using a chromatic threshold of 3 ΔS and an achromatic threshold of 4 ΔS . The scale on the top right of the images indicates the stimulation of the UV receptor channel

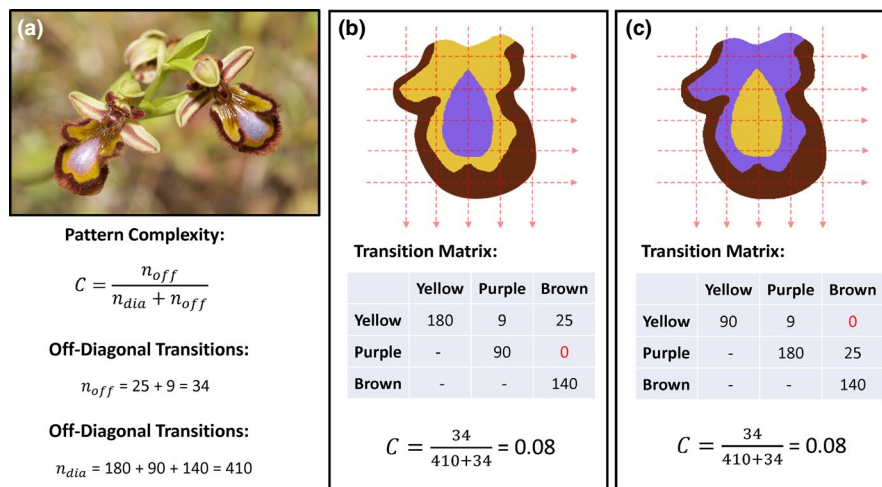


FIGURE 5 (a) *Ophrys ciliata*, a bee mimicking orchid (Vereecken, 2008). (b) Measuring colour pattern complexity as the proportion of off-diagonal transitions in the transition matrix resulting from horizontal and vertical transects (red dotted lines) across the segmented central flower pattern as seen in (a). The diagonal transitions (synonymous) are proportional to the relative size of the colour pattern elements whereas the off-diagonals are proportional to the amount of border colour pattern elements share. (c) Measuring colour pattern complexity of a hypothetical mimic. While the transition matrix clearly captures the difference between colour pattern (b) and (c), the complexity of the two patterns is identical. Image credit Figure 5a: Nicolas Vereecken

2012 for detailed discussion). For example, in many cases of mimicry, the mimic only replicates the presence or absence of model colours in their patterning, without precisely matching the model's spatial

arrangement (e.g. Winters et al., 2018). To human observers, this imperfect mimicry might be immediately apparent, but the intended receiver is unable to distinguish between model and mimic (Chittka &

Abundance Weighted Mean Saturation Contrast:

$$M_{\Delta S_{Sat}} = \sum_{i=1}^k f_i \Delta S_{Sat,i}$$

Number of Colour Pattern Elements:

$$k = 3$$

Relative Abundances Morph A:

$$f_{brown} = 0.34 \quad f_{yellow} = 0.44 \quad f_{purple} = 0.22$$

Relative Abundances Morph B:

$$f_{brown} = 0.20 \quad f_{yellow} = 0.70 \quad f_{purple} = 0.10$$

Colour Patch Saturation:

$$\Delta S_{Sat,brown} = 1.5$$

$$\Delta S_{Sat,purple} = 4.3$$

$$\Delta S_{Sat,yellow} = 8.9$$

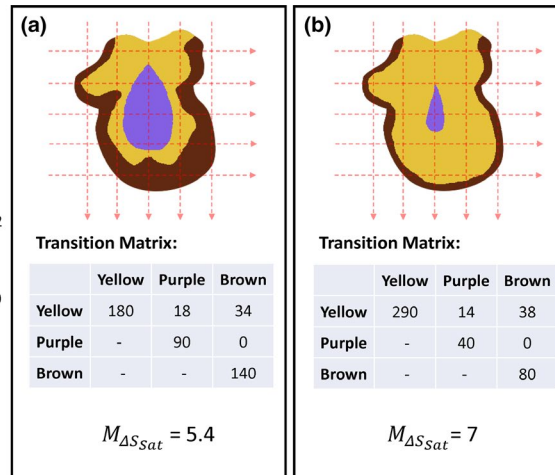


FIGURE 6 Using visual contrast analysis to quantify differences in appearance of a hypothetical polymorphism in *Ophrys ciliata* (Figure 5a). Average saturation (distance from the achromatic point in the log-transformed RNL colour space, ΔS_{sat}) in the colour pattern can be expressed as an abundance weighted mean. The relative abundance of each colour pattern element can be calculated as the proportion of diagonal transitions compared to the sum of all diagonal transitions (f_i). (a,b) Note how the off-diagonal transitions between morphs change marginally in comparison to Figure 5, however, the level of overall colour pattern saturation for this kind of polymorphism differs substantially due to the increased relative abundance of saturated yellow, calculated as the relative abundance of yellow - yellow transitions in the diagonal of the transition matrix (f_{yellow})

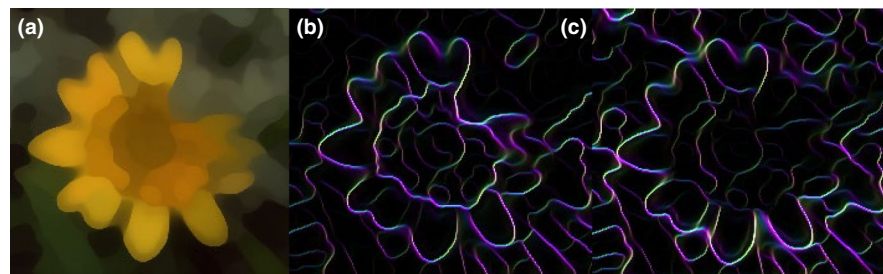


FIGURE 7 (a) The RNL filtered flower from Figure 4c. (b) Edge intensities of chromatic ΔS contrast. Different colours indicate different angles of hypothetical edge detecting receptive fields, the intensity reflects the contrast. (c) Edge intensities of achromatic (luminance) ΔS contrast. Colours show edge angle whereas intensity shows edge strength

Osorio, 2007; Dalziel & Welbergen, 2016; Mallet & Joron, 1999). In a hypothetical case, CAA could be used to quantify imperfect sexual mimicry of orchids (Figure 5) where the plant mimics the visual and chemical appearance of a potential mate (e.g. Gaskett & Herberstein, 2010; Vereecken, 2008). For further discussion of the biological relevance, worked examples, potential future investigations, and guidance on parameter choices see Endler (2012), Rojas, Devillechabrolle, and Endler (2014), Ligon et al., (2018) and Winters et al. (2018). For details on CAA parameters available in QCPA see the Supplemental Material.

2.6.2 | Visual contrast analysis

Visual contrast analysis (VCA) is designed to investigate colour, pattern and luminance simultaneously by providing pattern statistics which combine spatial and chromatic properties of colour patterns such as abundance weighted chromaticity measures (Endler

& Mielke, 2005, Supplemental Material). The perception of visual contrast is a combination of spatial (relative size and position of colour pattern elements), chromatic (hue and saturation), and achromatic (luminance) properties of a colour pattern due to lower and higher level neuronal processing of visual information (e.g. Pearson & Kingdom, 2002; Shapley & Hawken, 2011; Simmons & Kingdom, 2002; White et al., 2017; Willis & Anderson, 2002). Furthermore, interactions between the absolute and relative size of colour pattern elements and their chromatic and achromatic properties includes simultaneous colour contrast and colour constancy mechanisms that are understood in very few visual systems (e.g. Simpson, Marshall, & Cheney, 2016). VCA provides a set of metrics that are designed to capture some of these effects. We have adapted some of these metrics to use known or assumed colour opponency mechanisms to measure chromaticity (Supplemental Material). Using the previous orchid example, VCA could be used to investigate how polymorphism in our hypothetical population interacts with pollinator



FIGURE 8 Colour map in a log-transformed Receptor Noise Limited Model (RNL) chromaticity space of the non-UV information in Figure 5c. The axes are automatically labelled based on the names of the receptor channels used to create each dimension of colour, for example the X-axis (RNL X dimension) is mw:lw, showing that mw-dominant colours are on the left, and lw-dominant colours are on the right of the plot. X and Y are defined in equation 4 of Hempel de Ibarra et al. (2001). Darker parts of the cloud indicate more pixels in that ROI are located at that coordinate. The boundary around each ROI pixel cloud reflects 1 ΔS . In this case, the flower and its background do not overlap. For tetra-chromatic colour maps, the Z-axis is represented as a stack of X&Y maps (see Supplemental Material)

learning or differences in attractiveness to pollinators (Figure 6). See the Supplemental Material, original publications (Endler, 1991; Endler & Mielke, 2005) and empirical studies (Endler & Houde, 1995; Sibeaux, Cole, et al., 2019, 2019) for further information.

2.6.3 | Boundary strength analysis

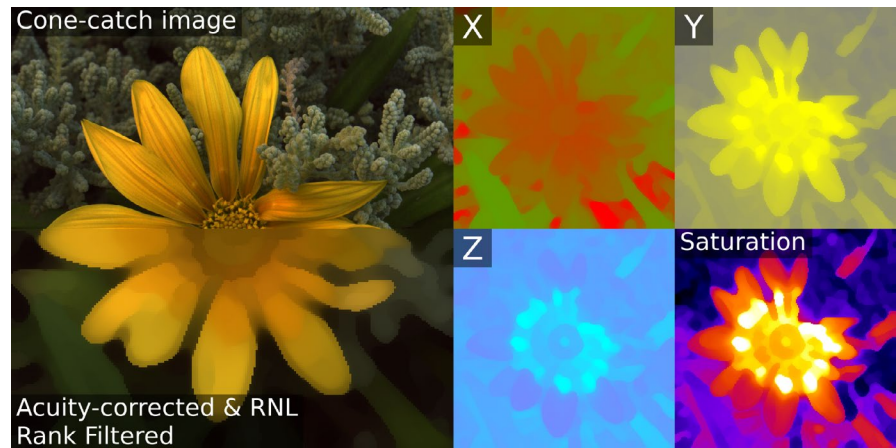
Boundary strength analysis (BSA, Endler et al., 2018) is an extension of CAA (Endler, 2012). The transition matrices generated in the process of adjacency analysis can be used to measure properties

of boundaries between colour pattern elements. The underlying argument for this type of analysis is that the relative size, abundance, colour, brightness and adjacency of the patches within a colour pattern, and the chromatic or achromatic contrast of the boundaries between adjacent patches, influence its signalling properties (Endler et al., 2018; Green et al., 2018; Shapley & Hawken, 2011). These parameters also define the properties of the edges between and within parts of visual scenes and textures. BSA (as well as CAA and VCA) is also capable of quantifying possible effects of viewer perspective and movement (Endler et al., 2018). For a detailed introduction to BSA, possible future research and guidance on parameter choices, please refer to the original publication (Endler et al., 2018) and empirical studies using BSA (e.g. Sibeaux, Cole, et al., 2019, 2019). For detailed equations and information on modifications of parameters since original publication, see the Supplemental Material.

2.6.4 | Local edge intensity analysis and ΔS edge maps

Boundary strength analysis depends on a segmented image with clearly delineated (clustered) colour pattern elements (Endler et al., 2018). However, the segmentation process removes a large degree of subthreshold information, particularly smooth gradients of brightness and colour which the viewer may perceive. For this purpose, we provide LEIA, as a way of quantifying edge properties in an image or ROI (Region of interest) that does not rely on a segmented input. By comparing each pixel to its horizontal, vertical and diagonal neighbours LEIA quantifies edge intensities in terms of colour and luminance contrast in log-linear RNL opponent space (Renoult et al., 2017). The result can be visualized as ' ΔS Edge Images' (Figure 7). BSA weights the strength of boundary classes according to their global (across an entire image or ROI) relative abundance, whereas LEIA provides a local measurement of edge intensity on roughly the scale of an edge detecting receptive field. This approach allows one to consider edge contrast at the scale of the functional units (receptive fields) at which low level edge and feature detection are thought to take place (Marr, 2010; Marr & Hildreth, 1980). While LEIA is suited to the investigation of similar aspects of colour pattern design and function as BSA, it can do this without the need for clustering an image, while using a more neurophysiological approach than BSA. We recommend that LEIA should be used on images which have first been controlled for acuity (to remove imperceptible edge/gradient information) and images which have also been through the RNL ranked filter, so that local chromatic and luminance edges have been reconstructed to their maximal values. LEIA also provides numerical output describing the distribution of edge intensities across an image. These parameters are specifically designed to be robust in the case of non-normally distributed edge intensities in an image (e.g. a small conspicuous object on a homogeneous background). Local edge contrast can be visualized as ΔS edge intensity images (Figure 7b,c).

FIGURE 9 An example of the red-green ($lw:mw$) opponent channel (X), blue-yellow ($(lw + mw):sw$) channel (Y) and the UV channel (Z) where the colour indicates the position of a pixel along that axis. The saturation map shows the Euclidean distance of each pixel to the achromatic point



2.7 | Step 7: Data visualization

We provide a range of novel approaches for data visualization. Calibrated digital photography and the coupled transformation of image data into psychophysical colour spaces provides a challenge but also an opportunity for visualization. We have already introduced the ΔS edge intensity images and extend that selection with colour maps, XYZ opponency images and saturation images.

2.7.1 | 'Colour maps' and 'XYZ chromaticity and saturation images'

The representation of chromatic information in colour spaces is a useful tool for data visualization in visual ecology (Endler & Mielke, 2005; Gawryszewski, 2018; Maia, Eliason, Bitton, Doucet, & Shawkey, 2013; Renoult et al., 2017). To date, most studies present their data as a scattering of points, which are either discrete measurements taken with spectrometers, or the mean centroids of image ROI cone-catch values. Techniques such as area or volume overlap between point clouds, or permutation analysis are then used to determine how dissimilar two colour patches are (e.g. Endler & Mielke, 2005; Kemp et al., 2015; Maia & White, 2018; Stoddard & Prum, 2008).

Colour space data visualizations generally do not incorporate any spatial (colour pattern) information. The use of calibrated digital imaging provides thousands, or even millions of colour measurements within each ROI, capturing the entire range of chromatic gradients present in any natural pattern. Using the log transformed opponent colour space (Hempel de Ibarra et al., 2001; Kelber, Vorobyev, & Osorio, 2003; Renoult et al., 2017), we provide representations of spatio-chromatic information in a perceptually calibrated colour space. 'Colour Maps' allow for the representation of entire visual scenes in a chromaticity diagram, in addition to the abundance of colours across part of the image (Figure 8). Among other purposes, colour maps may be used for visualizations and investigations of chromatic background matching. The overlap of ROIs in colour space can be expressed as an abundance weighted percentage. QCPA integrates tools which enable colour maps to be flexibly combined and

compared between image sections, or measurements taken from multiple images.

We also introduce the ability to convert cone-catch images to RNL XYZ chromaticity and saturation images, allowing visualization and measurement of the independent axes of colour in a di- tri- or tetra-chromatic image (showing the Euclidean distance of each pixel's RNL XYZ axes coordinates), in addition to generating a saturation image (Euclidean distance of each pixel to the achromatic point) (Figure 9).

2.7.2 | Step 8: Interpreting QCPA output

Quantitative Colour Pattern Analysis provides a huge range of metrics from each image (currently 181 parameters). Some of these parameters likely correlate well with aspects of animal evolution, behaviour and neurophysiology, while others are likely to show no signal. Likewise, some parameters will operate synergistically with each other, while others are independent or antagonistic. Moreover, these relationships could be fundamentally different between taxa, meaning caution should be used when comparing results between highly divergent taxa (such as vertebrate vs. invertebrate systems). QCPA can be used to address specific hypotheses linking one or a small subset of parameters (e.g. mean animal vs. background luminance contrast) to a response variable (e.g. predator attack rates) based on the context of the task. Such experiments require highly calibrated environments and stimuli where confounding influences on the perception of specific spatial, chromatic or temporal properties of a visual stimulus are controlled for (reviewed in Shapley & Hawken, 2011). However, colour patterns can be quantified in a great number of parameters, all of them capturing different aspects of chromatic, achromatic and spatial properties or combinations thereof (of which QCPA only captures a few).

Commonly used terms such as 'Complexity', 'Conspicuousness' or 'Similarity' should be considered as umbrella terms describing perceptual consequences caused by the variation of physical properties of colour patterns and their visual backgrounds (which often cannot be described by a single parameter). The lack of empirical testing of many QCPA parameters (and those of most other pattern analyses) makes it hard to offer broad recommendations for parameter choice

TABLE 1 A comparison of the Quantitative Colour Pattern Analysis framework to other existing pattern analyses and frameworks. For patternize see van Belleghem et al. (2018). For PAT-GEOM see Chan, Stevens, and Todd (2018). For PAVO see Maia et al. (2019). For NaturePatternMatch see Stoddard et al. (2014). For Colourvision see Gawryszewski (2018). We would also like to point out an approach by Pike (2018) which shares similarities with NaturePatternMatch

| | QCPA | MICA | Patternize | PAT-GEOM | PAVO 2.0 | Colourvision | NaturePatternMatch |
|---|--------|--------|------------|----------|----------|--------------|--------------------|
| Modelling of non-human Photoreceptor stimulation | ✓ | ✓ | | | ✓ | ✓ | |
| Modelling of visual acuity | + | | | | | | |
| Visual Contrast Analysis | + | | | | | | |
| Local Edge Intensity Analysis (LEIA) | ★ | | | | | | |
| Adjacency Analysis | + | | | | ✓ | | |
| Boundary Strength Analysis | ✓ | | | | ✓ | | |
| Bandpass based pattern analysis | | + | | | | | |
| Alternative pattern metrics | ★ | ★✓+ | ✓ | + | | | |
| Landmark based pattern analysis | | | + | | | | + |
| Image segementation using perceptual thresholds | ★ | | | | | | |
| Alternative image segmentation tools | + | + | ✓ | | ✓ | | |
| Plotting colours in colour space | + | | | | + | + | |
| Plotting of spatiochromatic information in colour space | ★ | | | | | | |
| Graphical user interface | | | | | | | |
| Software/Language | ImageJ | ImageJ | R | ImageJ | R | R | C++ (Matlab) |

✓ Adapted as per original scientific publications

✚ Substantially modified

★ Novel concept or methodology

across the huge diversity of possible contexts, especially when making observations in natural or nature-like levels of spatio-chromatic complexity. The ‘simpler’ the research question and the more controlled the experiment, the more adequate it is to consider one or a few pattern parameters in isolation.

Therefore, when there is no a priori reason to choose specific parameters, we recommend the use of multidimensional data analyses, such as principal component analysis (PCA), metric- and non-metric multidimensional scaling (MMDS/NMDS) or similar multivariate approaches such as factor analysis to identify correlations between pattern analysis output and animal behaviour (e.g. Sibeaux, Cole, et al., 2019, 2019) or to distinguish between taxa (e.g. Chan et al., 2019; Ligon et al., 2018; Winters et al., 2018). Doing so can be thought of as operating in a multidimensional pattern space (for discussion see Cuthill, 2019 and Stoddard & Osorio, 2019). Such a pattern space can include categorical data (e.g. presence/absence), data from other pattern analyses (Table 1) as well as environmental data.

Reducing the dimensionality of such data comes with considerable statistical challenges. However, it is possible to avoid many issues such as bias from the structure of datasets or false positives (e.g. Benjamini & Hochberg, 1995; Osborne, Osborne, Costello, & Kellow, 2011). While obvious for the use of QCPA, interpreting many potentially interacting pattern parameters is of increasing importance given a steadily growing diversity of analytical methods (Table 1) and the desire to incorporate effects of higher-level processing of visual information into the analysis of visual signals.

3 | DISCUSSION

Quantitative Colour Pattern Analysis is a framework for the analysis of colour patterns in nature at an unprecedented quantitative and qualitative level. At its core, QCPA uses the advantages offered by calibrated digital photography to enable the use of existing

spatio-chromatic colour pattern analyses (Figure 1). It also improves existing methodologies used in visual ecology by introducing a user-friendly and open-source framework which incorporates the ability to contextualize visual scenes according to photoreceptor spectral sensitivities, receptor noise levels and abundances, natural light environments, complex natural backgrounds, spatial acuity and viewing distance (Table 1).

The individual modelling components of QCPA rely on approximations and assumptions, which are based on our best current understanding of the underlying biological processes. As such, it is important to be aware of the limitations and underlying assumptions of the individual components of QCPA, some of which we discuss. QCPA makes extensive use of the receptor noise limited model (RNL) which has been behaviourally validated in various species including: humans, honeybees, birds, lizards, reef fish and freshwater fish (e.g. Champ, Vorobyev, & Marshall, 2016; Escobar-Camacho, Marshall, & Carleton, 2017; Vorobyev et al., 2001; Vorobyev & Osorio, 1998). However, the RNL model and RNL colour space is one of various available visual models and colour spaces that have also considered behavioural context to some degree and which may be considered as alternatives (reviewed in Gawryszewski, 2018; Renoult et al., 2017).

The RNL model (or any other visual model) is unlikely to represent the perceptual complexity of natural visual scenes for all species across all light regimes. To avoid making false assumptions, it is necessary to consider the perceptual context in which it is applied and how this context may violate model assumptions (Kelber, 2019; Lind, 2016; Olsson et al., 2018; Price, Stoddard, Shevell, & Bloch, 2019). For example, behavioural experiments have shown varying sensitivity to differences in colour in specific quadrants of colour space relevant to the behavioural ecology of species (Caves et al., 2018; Sibeaux, Cole, & Endler, 2019; Sibeaux, Keser, Cole, Kranz, & Endler, 2019). Another aspect that needs further investigation is the question of how distances in RNL colour space scale with behavioural thresholds across a wide range of visual systems and perceptual contexts (e.g. Fleishman et al., 2016). QCPA applies the log-transformed RNL colour space to minimize, but not remove, the impact of such threshold distortions (Gawryszewski, 2018; Vorobyev et al., 2001; Vorobyev & Osorio, 1998). Overall, the less validated model parameters are and the more profound assumption violations may be, the more likely deviations from the assumption that 1 ΔS equates to a behavioural threshold (e.g. a 75% success rate in a pairwise choice paradigm) will occur. Furthermore, the photopic version of the RNL, which is used here was developed to model colour discrimination near the achromatic point under photopic conditions (Vorobyev et al., 2001; Vorobyev & Osorio, 1998). However, when visual systems operate in crepuscular or scotopic conditions, the retinal stimulation to visual information becomes the result of both cone and rod stimulation or rod stimulation only (Kelber, Balkenius, & Warrant, 2002; Olsson et al., 2015; Osorio et al., 2004; Veilleux & Cummings, 2012; Vorobyev & Osorio, 1998). Another example highlighting context-specific threshold modelling is the distinction between detection and

discrimination thresholds which has direct implications on the application of the RNL (Lind, 2016; Price et al., 2019).

Quantitative Colour Pattern Analysis enables the application of known sensory limitations to filter the information that is subsequently processed by low-level vision. While a range of parameters provided by the QCPA have been shown to be of importance in some species, many remain to be applied and investigated in a broad range of behavioural contexts and visual systems. To what extent the observed parameterization of visual information bears ecological or behavioural significance subsequently must be inferred and calibrated using behavioural experimentation (Olsson et al., 2018). QCPA provides numerous parameters based on concepts shown to be relevant to a range of natural contexts (Endler, 1991, 2012; Endler et al., 2018; Endler & Houde, 1995; Rojas et al., 2014; Rojas & Endler, 2013; Sibeaux, Cole, et al., 2019, 2019; Winters et al., 2018). However, it also provides parameters which are yet to be validated, particularly on a quantitative scale. This provides great potential for future research as well as parameter calibration using behavioural experiments and highlights the importance and feasibility of a reductionist approach to the quantification of colour patterns and their function (*sensu* Stoddard & Osorio, 2019). Given the ability to link QCPA parameters and animal behaviour, we encourage the use of QCPA to design carefully calibrated behavioural experiments in the context of complex colour patterns and visual backgrounds.

There is considerable potential to improve QCPA by continuing to refine, test and develop its components. For example, we currently have not considered the loss of spatial and chromatic information due to light scattering or absorption, particularly in aquatic or dusty environments (e.g. Nilsson, Warrant, & Johnsen, 2014). Furthermore, many animal eyes do not have uniform retinas which, in combination with diversity in eye movements and eye shapes, leads to a little investigated diversity of visual perception in addition to the already discussed perceptual diversity in animal visual systems (Daly, How, Partridge, & Roberts, 2018; Hughes, 2018; Land, 1999; Land & Nilsson, 2012; Sibeaux et al., 2019; Willis & Anderson, 2002). QCPA could also be adapted to investigate moving patterns (e.g. Endler, 2012; Endler et al., 2018), given recent advances in the understanding of colour pattern functionality in the context of motion (Cuthill, Matchette, & Scott-Samuel, 2019; Fleishman, 1986; Hughes, Troscianko, & Stevens, 2014; Murali, 2018; Nityananda et al., 2018; Ramos & Peters, 2017; Umeton, Tarawneh, Fezza, Read, & Rowe, 2019). There are types of visual information we have barely begun understanding, such as polarization vision, the use of fluorescence as well as their interaction with an animal's perception of colour and brightness (Foster et al., 2018; Marshall, Cortesi, de Busserolles, Siebeck, & Cheney, 2019; Marshall & Johnsen, 2017; Smithers, Roberts, & How, 2019).

Recent years have seen a growing diversity of colour pattern analyses (Table 1). While some use conceptually similar pattern statistics to QCPA, others provide alternative approaches such as scale invariant feature (SIFT) analysis-based metrics (Lowe, 1999) and combinations with models to describe cognitive aspects of attention (Rosenholtz, Li, Jin, & Mansfield, 2010). The concept of QCPA-based pattern analysis

is entirely compatible with any of these methods. In fact, QCPA does not currently include any computer vision-mediated object recognition or figure-ground segregation. However, QCPA provides a promising platform for future implementations of computational approaches to higher level neuronal processing of visual information (e.g. Serre, 2014).

Quantitative Colour Pattern Analysis provides an unprecedented level of accessibility and user-friendliness by being free, open-source, graphical user interface mediated and accompanied by a vast body of support material. QCPA presents a comprehensive, dynamic and coherent work process starting with the acquisition of calibrated digital images and ending with the extraction of behaviourally and neurophysiologically contextualized pattern space. ImageJ has been the software platform of choice for image analysis for decades. Its architecture minimizes the risk of non-compatibilities due to future patches of co-dependent packages (often seen in R or Matlab) making QCPA (and MICA) well equipped for the future. ImageJ and MICA provide their own, rich, sets of image and pattern analysis and manipulation tools that QCPA profits from and can interact with. For example, GabRat (Troschianko et al., 2017) can be used in combination with QCPA to investigate chromatic aspects of disruptive colouration in the context of spatial acuity. Furthermore, it is possible to use QCPA and MICA with a simple smartphone or cheap digital camera and a colour chart for calibration. While it is advantageous to have access to spectrophotometry for comparison of modelling output, this is no longer a requirement and reduces the cost for equipment drastically.

In conclusion, there are many theories and predictions regarding the design, function and evolution of colour patterns in nature which, if at all, have only been investigated in comparably simplistic or qualitative ways. QCPA provides a powerful framework to investigate these theories in a novel quantitative and qualitative context.

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AUTHORS' CONTRIBUTIONS

C.P.v.d.B and J.T. conceived and tested the QCPA framework based on an original concept by C.P.v.d.B. J.T. wrote the software code and conceived the original (chromatic) RNL clustering and RNL-ranked filter algorithms, with further testing, debugging and conceptual input and modification by C.P.v.d.B. C.P.v.d.B and K.L.C. conceived the combination of chromatic and achromatic discrimination thresholds for image segmentation. C.P.v.d.B. wrote the MATLAB precursor of the QCPA user interface and pattern analysis which contains the original code by J.A.E. J.A.E. also contributed many of the original concepts, J.A.E., K.L.C and N.J.M. have contributed to conceptual discussions and manuscript review.

DATA AVAILABILITY STATEMENT

The latest version of QCPA and its open source code (JAVA script) are available for download as part of the MICA toolbox at www.empiricalimaging.com.

The website provides detailed manuals, tutorials, FAQs, a dedicated forum and updates. If you intend to use QCPA and/or the micaToolbox, please use the website to familiarise yourself with the latest updates. We do encourage users to use the website and the Supplemental Material as their primary source of information on how to use QCPA. The version of the code used at the time of publication can be found at <https://doi.org/10.5281/zenodo.3517896> (troschianko, 2019). A fully functional MATLAB based precursor of QCPA can be accessed at <https://doi.org/10.5281/zenodo.3518682> (van den Berg, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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