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Forest light and its influence on habitat selection

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Abstract

Light filtered through the forest canopy is the most variable physical factor in tropical forests, both in space and time. Vegetation geometry, sun angle, and weather generate five light environments, which greatly differ in intensity and spectrum. Forest light spectra can directly affect photosynthesis, plant morphogenesis, visual communication, and the effectiveness of plant-animal interactions. For animals, the apparent simplicity of five light environments is complicated by different types of contrast with the optical background which greatly modify the conspicuousness of visual signals. The purpose of this paper is to describe peculiarities of light in tropical forest, and to review the effects of light intensity and especially quality on plants and animals. Ecophysiological adaptations of plants to cope with contrasting light environments operate at daily, seasonal and life time-scales. Ambient light quality acts as a signal for both animals and plants, and consequences on plant growth, colour display, and signal design are examined. An analysis of the range of spectral parameters along a deforestation gradient is presented, testing if sites with more variation in light could support more species which are light-environment specialists. It is suggested that light quality measurement may be used to estimate the structural impact of forest exploitation, and that gives us the information necessary for a functional explanation of anthropogenic effects on tropical forest diversity.

Introduction

There has already been considerable research and recent syntheses on the subject of light in tropical forests, and on its consequences for animals and plants (e.g., Hailman 1977, 1979; Endler 1993; Vasquez-Yanes & Orozco-Segovia 1993; Chazdon et al. 1996; Fleishman et al. 1997; Bongers & Sterck 1998; Bradbury & Vehrencamp 1998 and references therein). Light measurements are relatively scarce in forest canopies (e.g., Hailman 1977, Endler 1993; Fleishman et al. 1997), mostly due to the difficult access and to the high spatial and temporal variation of light, but light filtered through the forest canopy has been measured in various ways. In plants, knowledge of light effects has considerably progressed with the identification of the wavelength-sensitive photoreceptors, a task which is still under way (reviews in Smith 1995; Fankhauser & Chory 1997; Tanada 1997; Ahmad 1999). Similarly, questions about crypsis and conspicuousness of colour signals have been only ap-

propriately addressed in tropical forests following the development of spectroradiometry (e.g., Endler 1990, 1991, 1993; Fleishman et al. 1993, 1997; Endler & Théry 1996; Craig et al. 1996; Regan et al. 1996, 1998) and a better understanding of visual systems (e.g., Osorio & Vorobyev 1996; Fleishman et al. 1997; Regan et al. 1996, 1998).

In this paper, the characteristics of light and the variation of light environments in tropical forest are summarized. Results show that variation of both light intensity and quality is perceived by wavelength-sensitive photoreceptors of plants, and that the repair of plant damage by high UV radiation also depends on the quality and timing of light in the environment. Adaptation of plants to light damage is examined, suggesting important consequences for niche differentiation. The effects of light environments on crypsis and conspicuousness of colour signals are reviewed, showing the potential for habitat selection and sensitivity to forest disturbance. Because forest light spectra can directly affect plant and animal growth and reproduc-

tion, light measurement may provide a functional explanation of anthropogenic effects on biodiversity. To test this hypothesis, a recent study showing that spectral diversity predicts bird and plant species diversity along a human disturbance gradient is reported.

Light availability in tropical forests

Two types of ambient light-flux measurements can be taken, each differing in the acceptance angle of the sensor: 'irradiance' (i.e., the total amount of light incident on a surface measured at 180° and including diffuse light) and 'radiance' (i.e., the energy flux emitted from a specific area at a small acceptance angle – see Endler 1990; Bradbury & Vehrencamp 1998). Total irradiance (i.e., total light intensity) is obtained by integrating the irradiance spectra between 400 nm and 700 nm, yielding photosynthetically active radiation (PAR). The radiance of a colour patch in a particular light environment is the product of the irradiance (ambient light) spectrum and the intrinsic reflectance spectrum of the measured patch.

Total irradiance received by tropical forest canopy is more intense than at higher latitudes, due to higher solar declination closer to the equator (Mulkey et al. 1996). Light intensity frequently reaches instantaneous values of 1800–2200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at midday, with highest measured values of 2600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Wright & Colley 1994; Chazdon et al. 1996). However, cloudy weather can reduce PAR by 75% or more (Lee & Downum 1991). Although annual variation in photoperiod and sun angle yield maximal sun radiance at the summer solstice, highest irradiance is usually received by the canopy during the dry season because of reduced cloud cover (Chazdon & Fetcher 1984; Rich et al. 1993; Mulkey et al. 1996). As radiance of clouds is larger than that of blue sky (Endler 1993), light intensity in forest shade increases when the sun is obscured by a cloud (Anderson 1964; Evans 1966; Endler 1993). With cloudy weather, ambient light also contains relatively more photons at photosynthetically active wavelengths than forest shade with clear sky (Endler 1993).

Light intensity is greatly reduced when passing through the highest canopy layer, and then gradually decreases further in the understorey (Yoda 1974; Koop & Sterck 1994). Light extinction can be as high as 94% over the first 5 m (Johnson & Atwood 1970). Mean light intensity levels of 0.1–1.9% of full sunlight have been reported at ground level, where

sunflecks contribute to the highest mean value (review in Bazzaz & Pickett 1980). This reduction of light quantity coincides with drastic changes of direct sunlight spectrum induced by selective transmission and reflection by leaves. The ultraviolet (UV) part of the spectrum is almost completely absorbed, as well as most of the visible wavelengths with the exception of those between 520 and 620 nm (review in Endler 1993), and a larger proportion of the infra-red (IR) is reflected and transmitted by leaves (e.g., more than 30% reflectance and 40% transmittance between 700 and 1100 nm – Gates 1965). Despite the high spatial and temporal heterogeneity of light in forests, forest geometry, weather, and sun angle define a limited number of spectral light environments (Endler 1993; Figure 1). At dawn and dusk, and during transitions with daylight, when the sun is less than about 10° above the horizon, ambient light is enriched in the purple wavelength; the deficiency in middle wavelengths (570–630 nm) is caused by light absorbance by atmospheric ozone, particularly around 604 nm (Rozenberg 1966; McFarland & Munz 1976; Endler 1993). Light in large gaps and open areas is whitish. Light in small gaps is yellow-orange (through hole that subtend a solid angle of less than 2° to the vertical, e.g., from a 30 m canopy this would represent a 1 m diameter sun patch; Endler 1993). The spectrum of 'forest' shade is greenish to yellow-green, because most of the ambient light is from sunlight reflected by, and transmitted through, leaves between 520 and 620 nm, with little or no ambient light from the sky, and none at all from the sun. In 'woodland' shade, where forest canopy is more discontinuous and a larger proportion of blue sky is visible from the forest floor than in forest shade, the light spectrum is bluish to bluish-grey. The spectrum of small gaps, woodland shade, and forest shade converge to white with cloudy weather (Endler 1993; Figure 1). Spatial and temporal variations of these five heterogeneous light environments define the availability of light to forest plants and animals. However, the relative simplicity of five light environments is much more complex for animals: crypsis and conspicuousness will also be affected by transmission and reception of light signals (review by Bradbury & Vehrencamp 1998). Some of these effects for animals, like background radiance and contrast, countershading, or pattern contrast, are presented later in the paper.

Light is also polarized in tropical rain forest (Shashar et al. 1998). Among light environments, woodland shade and open areas are dominated by

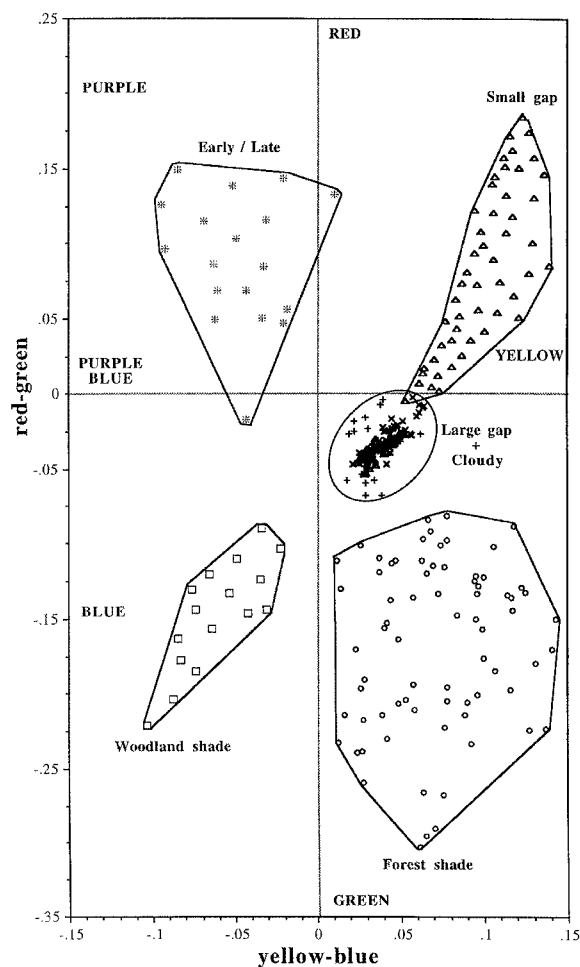


Figure 1. Colour variation of ambient light in primary tropical rain forest of French Guiana. Each point represents a single irradiance spectrum from which hue angle and chroma have been extracted using the segment classification method of Endler (1990) between 400 nm and 700 nm. The ordinate represents relative brightness of red and green spectral segments, and the abscissa is the difference between yellow and blue segments. The distance from the origin is chroma (colour saturation) and the angle clockwise from the top of the ordinate is hue (aspect of colour identified by words like 'red', 'green', and 'blue'). The direction of vectors approximately corresponding to Munsell (1975), hues are indicated by colour names. Light was measured between 11:00 and 13:00 about 50 cm above the forest floor at the Nouragues CNRS research station ($4^{\circ}05' \text{ N}$ - $52^{\circ}42' \text{ W}$), French Guiana. A PS-1000 Ocean Optics portable spectroradiometer was used with an irradiance detector head (cosine-corrected, 180° acceptance angle) connected to a $200 \mu\text{m}$ diameter fused silica fibre optic. Light environments were selected before measurement, and outlines and names of light environments are indicated on the graph. No cloud was visible in clear sky conditions, and blue sky was totally absent in cloudy conditions. Small gaps measured 30–90 cm in diameter; the transition between small gaps and large gaps is shown by decreasing chroma of small gaps. The gradients between small gaps and forest shade, woodland shade and forest shade, early/late and large gaps, and clear sky and cloudy conditions are not shown here.

celestial polarization, whereas small gaps and forest shade are depolarized. Nevertheless, polarized light penetrating forest understorey is still measurable in dense forest shade. Cloud coverage has little or no effect on light polarization in small gaps, forest shade or woodland shade, but depolarizes the light field in open areas and in large gaps. When light arrives through a small gap and not directly from the sun (woodland shade with small gap, see 'canopy hole shade' in Shashar et al. 1998), light is polarized at the orientation of the light source, and is not depolarized by cloud coverage.

Differences in the spectrum of forest shade have been related to leaf thickness, with thinner leaves leading to greater 'chroma' (colour saturation – Endler 1993). Because canopy leaves are thicker than understorey leaves (e.g., Oberbauer & Strain 1986; Lee et al. 1990; Strauss-Debenedetti & Berlyn 1994), forests with denser canopies may show lower chroma in forest shade. Sun and shade plants appear to have similar optical properties, but shade plants are more efficient than sun plants in absorbing light for photosynthesis (e.g., Lee & Graham 1986; Lee et al. 1990). To my knowledge, only one study has considered the influence of position within trees on the optical properties of leaves (Poorter et al. 1995). This study showed that the efficiency of light absorption increased as light level decreased, the efficiency of light absorption per unit leaf chlorophyll remained relatively constant, but the optical properties of leaves showed no significant difference with light environment.

Differences between light environments are much greater than variation in leaf colour. Consequently, the same light habitats are found in very different forests, although the relative frequency of these habitats will depend upon the forest and canopy geometry (Endler 1993, 1997). Forests with more opened canopies have more woodland shade, and those with denser and more continuous canopies have more forest shade. Within the same forest, both the frequency and size of gaps increase with height off the ground (Hubbell & Foster 1986; Koike & Syahbuddin 1993; Van der Meer et al. 1994). Therefore, canopy light habitats mostly consist of a mosaic of large gaps and woodland shade (Endler 1993). Woodland shade, which is only found in the canopy and in large treefall gaps in wet forests with dense canopy cover, can reach lower levels in drier forests with thin or defoliated crowns. The understorey of dense tropical forest is, in contrast, a mosaic of forest shade and small gaps.

Because of vegetation cover, the blue part of the spectrum, present in the canopy, disappears as distance from the canopy increases. In absolute intensity, the UV and IR wavelengths are also strongly reduced in the understorey compared to the canopy (e.g., Gates 1965). However, the intensity of near-IR wavelengths (far-red around 730 nm) is increased relatively to red wavelengths (around 660 nm) strongly reducing the red/far-red ratio, to which plants are sensitive, compared to open areas (Holmes & Smith 1977a, b; Lee 1987; Schmitt & Wulff 1993). Leaves absorb the most UV (e.g., Lee 1987), except in open or disturbed canopies where more diffused UV-rich light can penetrate (Brown et al. 1994). Endler (1993) also predicts more UV in woodland shade than in forest shade. As diffuse light contributes more to understorey light with cloudy weather than with clear sky, there may be relatively more UV in the understorey when clouds obstruct the sun.

Wavelength-sensitive perception of light by plants

As plant progress from seed to the adult stage, they have to respond to a wide range of light intensities and qualities over a variety of time scales, from seconds to daily cycles, to annual cycles and yearly variations (reviews in Bazzaz & Pickett 1980; Roach & Wulff 1987; Vasquez-Yanes & Orozco-Segovia 1993; Long et al. 1994; Chazdon et al. 1996; Bongers & Sterck 1998). Light variations are perceived by three photoreceptor systems responding in the UV (UV-B photoreceptors), blue/near-UV (cryptochrome photoreceptors), and red/far-red (phytochrome photoreceptors) spectral ranges (reviews in Fankhauser & Chory 1997; Ahmad 1999). Blue light responses include inhibition of production of chloroplasts and pigments, inhibition of the rate of hypocotyl growth, phototropism, stomatal opening, induction of gene expression, and morphogenesis (reviews in Endler 1993; Kendrick & Kronenberg 1994; Fankhauser & Chory 1997; Horwitz & Berrocal 1997; Ahmad 1999). A novel flavoprotein, NPH1, has been proposed as a photoreceptor for phototropism (Christie et al. 1998). The relative intensity of red to far-red light has been shown to affect seed germination, hypocotyl elongation, tillering rate, growth and elongation of stems, expansion rates of leaves, flowering, fruiting, and photosynthetic rates (reviews in Endler 1993; Kendrick & Kronenberg 1994; Smith 1995; Fankhauser & Chory 1997; Ahmad 1999). Even the high irradiance re-

sponses, which mostly require prolonged exposition to high light intensity between 710 and 720 nm (e.g., inhibition of hypocotyl elongation, leaf movement, flowering), are controlled by wavelength-sensitive photoreceptors in the red/far-red and blue spectral regions (Tanada 1997). Nevertheless, there appears to be complex interactions between and within these types of photopigments (Smith 1995; Fankhauser & Chory 1997; Horwitz & Berrocal 1997; Tanada 1997; Ahmad 1999). Phytochrome interacts with cryptochrome photoreceptors to potentiate blue-light signalling, and impacts on phototropism downstream of the NPH1 mediated signalling pathway (Ahmad 1999). Cryptochrome functions in photomorphogenesis and participates in phototropism through interaction with the NPH1 pathway (Ahmad 1999). Complete studies of these phenomena have been conducted in *Arabidopsis*, but little is known about plants in the wild, and even less about tropical canopy plants. However, in all cases studied, wavelength-sensitive photoreceptors perceive the intensity and colour of ambient light, allowing plants to respond to environmental cues.

Damage caused to plants by high irradiance in the canopy

The avoidance of high light-intensity stress is obtained by chloroplast movements, leaf movements (which include greater leaf angles at the top of the canopy), increased albedo, and photoinhibition (reviews in Demmig-Adams & Adams 1992; Long et al. 1994). Because of direct sunlight, canopy plants have to deal with high UV radiation in the canopy, which damages DNA (review in Britt 1996). Photoreactivation of DNA, obtained during subsequent exposures to UV-A and blue light, is the main line of defence plants have against UV-induced damage (Britt 1996). It reflects the action of photolyase enzymes, which are mediated by phytochrome pigments through successive expositions to red and UV lights. Therefore, the repair of plant damage by high UV radiation also depends on the quality and timing, as well as quantity, of light in their environment (Britt 1996).

Adaptations of plants to constraints of canopy light and consequences for habitat selection

Light is both a fundamental requirement and a constraint for canopy organisms. Many tree species with

access to deep soil water produce leaves and flowers during the dry season, benefiting from increased irradiance (Wright & Van Schaik 1994) or because it constitutes a relatively enemy-free temporal space. Similarly, several tree species benefit from this seasonal opportunity to produce leaves and improve carbon gain (review in Mulkey et al. 1996). Light is often in excess in the canopy, well above the light-saturation point of canopy species (Fetcher et al. 1987; Doley et al. 1988). However, light intensity can sometimes be limited by cloud cover, which frequently reduces irradiance on exposed leaves below photosynthetic light saturation (Oberbauer & Strain 1986; Pearcy 1987; Zotz & Winter 1993; Hogan et al. 1995), and which limits tree growth in wet forests during years of highest cloud cover (Schulz 1960; Alvim 1964).

Both the morphology and physiology of leaves show adaptations to canopy light. Leaves exposed in the canopy are thicker, more vertical, and have higher specific leaf mass, lower chlorophyll density and higher *a/b* ratio than understorey leaves (Oberbauer & Strain 1986; Givnish 1987; Pearcy 1987; Bongers & Popma 1988; Fetcher et al. 1994). Shade leaves being, in contrast, relatively enriched in chlorophyll *b*, their low chlorophyll *a/b* ratio shows increased chlorophyll and light harvesting per chloroplast (review in Chazdon et al. 1996). Canopy leaves have higher light-saturated photosynthetic rates than conspecific leaves positioned lower in the canopy, and pioneer species have higher light-saturation points than climax trees or shade plants (review in Chazdon et al. 1996). Light quality varies with light environments and position within the forest, so it is possible that morphogenetic processes may differ among species living in different light environments (Endler 1993). For example, critical levels of light intensity or quality could be reached in the canopy for shade-tolerant or shade-demanding species, but not for light-demanding species. Because of canopy light characteristics, canopy species should be better adapted to high irradiance, UV, and IR radiation. This is potentially a strong feature of habitat selection and niche differentiation.

Among tropical forest trees, shade-tolerant and light-demanding species are well recognized (review in Denslow 1987). Specific differentiation of trees in light habitats has been proposed (Denslow 1980, 1987) in contrast to the null hypothesis of random occupation of light habitats (Hubbell & Foster 1986). However, adult trees of both types occur in a wide variety of light intensities, and most species are not associated with a particular light habitat (e.g., Lieberman

et al. 1989, 1995; Welden et al. 1991). In a recent review of gap-size niche differentiation by tropical rain forest trees, Brown & Jennings (1998) showed that there are little evidence to support species differentiation according to gap size or light variation, and reviewed the numerous problems involved in detecting niche differentiation, notably inappropriate measurement and use of various gap sizes and light conditions in experiments. Similarly, Bongers & Sterck (1998) showed that there are too few data presently available on the light levels of trees larger than small saplings to form conclusion on the effective differentiation of tree species in light habitats compared with random occupation.

Pittendrigh (1948), who distinguished 'exposure', 'sun' and 'shade-tolerant' species, has described the vertical partitioning of light in epiphytic bromeliads. Each species group is characterized by morphological and physiological adaptations to light and water levels (Pittendrigh 1948; Benzing 1995). Species of the 'exposure' and 'sun' group are characterized by crassulacean acid metabolism (a photosynthetic pathway adapted to drought and high irradiance). Shade-tolerant species, in contrast, often have lower light-compensation and light-saturation points typical of C_3 photosynthesis (Benzing 1995). Because light availability decreases with cloud cover, the shade group is not represented at the wettest sites, and the exposure group prevails at sites with lower precipitation (Griffiths & Smith 1983). The dense growth of epiphytes in cloud forest can also be explained by variations of light intensity and spectrum compared to other tropical forests (Endler 1993). Physiological adaptation of not only epiphytes (Benzing 1995), but also of hemiepiphytes (Williams-Linera & Lawton 1995) and non-vascular epiphytes (Rhoades 1995), potentially contribute to species space-partitioning in relation to light availability.

Crypsis and conspicuousness of colour signals, and consequences for habitat selection

The transmission efficiency of a visual signal can be enhanced by four types of contrast with the optical background: brightness, colour, pattern and movement contrasts (Bradbury & Vehrencamp 1998). Each of these strategies for conspicuousness has an opposed contrast-reducing strategy for crypticity. In all cases, brightness, colour components of the ambient light irradiance, and background radiance spectra, greatly

affect the conspicuousness of a colour signal (Hailman 1979; Lythgoe 1979; Endler 1986, 1990, 1993; Endler & Théry 1996; Fleishman et al. 1997). These visual contrasts can be used in communication between animals (predation and crypsis; recognition of species, sex, and age; sexual selection), and in communication between animals and plants (herbivory, pollination, seed dispersal).

Brightness contrast is most efficient when backgrounds are extremely light or extremely dark, and may be influenced by the direction of illuminating light (Cott 1940; Bradbury & Vehrencamp 1998). For example, in *Phylloscopus* warblers from habitats of different brightness, numerous white patches increase brightness contrast in species from dark habitats, whereas species from bright habitats have no white patch and rely more on acoustic communication (Marchetti 1993). For animals illuminated from above, such as those in forest canopy, countershading can be used for concealment by lightening the ventral side, and reverse countershading can be used for conspicuousness by darkening the ventral side (Cott 1940; Hailman 1979). This greatly depends on the position of the viewer, either potential mate or predator (Endler 1990; Bradbury & Vehrencamp 1998). Colour contrast can be obtained by difference in either hue or chroma (colour saturation) between the visual signal and its background (Endler 1990). Therefore, the most conspicuous colours are those which are rich in ambient light wavelengths but poor in the background reflectance spectra (Endler 1990). If the ambient light is strongly coloured, as it often occurs in forests, animals should use a colour signal that matches the ambient light peak and surround themselves with complementary colours to maximize brightness contrast. In addition, animals can use complementary colours whose cut-offs are centred on the region of greatest ambient light intensity (Endler 1992). Forest canopy vegetation provides a strongly patterned background that can be exploited for either contrast or camouflage (e.g., disruptive colouration, Cott 1940). The visual background moves in a slow and sinusoidal motion when the wind blows through the vegetation, which animals can utilize to hide from prey (e.g., vine snakes; Fleishman 1985). Contrast against this moving background can also be used to detect prey or to increase conspicuousness of a display (e.g., *Anolis* lizards, Fleishman 1992).

Canopy light consists of a mosaic of large gaps and woodland shade which greatly modifies brightness and colour contrasts between signals and backgrounds. In

open areas, and above and within the canopy, ambient light is whitish and rich in UV, and the background mostly consists of bright blue and UV sky. Therefore, conspicuous signals in such large gaps should be black for brightness contrast (Hailman 1979). No easy prediction can be made for colour contrast in white light, although a slight disadvantage to blue and possibly green colouring, and also to utilization of a blue background, may result from the reduction of light irradiance below 450 nm (Endler 1993). In canopy shade (woodland shade), ambient light is relatively rich in blue and UV, and background colour mostly consists of green leaves reflecting little UV (Fleishman et al. 1997). Consequently, colour signals in canopy shade should be blue, blue-green or UV to maximise brightness contrast, with some red or orange for increased contrast with the green background (Endler 1993). Because canopy light irradiance is richer in UV than forest shade, and because background radiance is green and poor in UV in both habitats, there should be more UV signals for communication in the canopy compared to heavily shaded environments (as shown by Fleishman et al. (1993) in *Anolis* lizards of Puerto Rico). Because woodland shade is most often found in the canopy, and forest shade in the understorey, there should be a vertical stratification of colours, with blue and blue-green hues used more often in the canopy and red or orange closer to the floor (Endler 1993). There is support for this hypothesis among 233 rain forest bird species of French Guiana, with brighter and bluer reflectance spectra in birds living within the canopy, and darker and redder colours of understorey birds (D. Gomez pers. com.). Colour saturation (chroma) can also potentially affect conspicuousness in different light habitats: patches on the body which are highly chromatic will be less sensitive to changes in ambient light than those with low chroma (which will change dramatically in both hue and chroma in different light environments) (Endler 1993, 1997). Consequently, species that need to be cryptic in different light habitats should have low chroma patches that change with the background as ambient light fluctuates. Species that need to be conspicuous could choose low chroma if they display in specific light environments, or high chroma that retain their contrast and hue independent of light environment (Endler 1997). If colour signals are brighter and more chromatic in the canopy, they will also be relatively insensitive to spectral variation of light habitats. However, too few species have been studied to confirm or invalidate this hypothesis on chromatic variation (Endler 1997).

Different flower, fruit or animal colours are more conspicuous in some tropical forest light environments and backgrounds, and less in others (Endler 1993; Craig 1996; Endler & Théry 1996). For example, it is noteworthy that blue fruits are most often displayed in open areas of high light intensity (Cooper et al. 1986). This may be explained by increased conspicuousness of blue signals in woodland shade compared to other light habitats (Endler 1993, 1997), or by the fact that it takes a 100 fold increase in light intensity to stimulate the blue cones in primate retinas that it does to stimulate the cones sensitive to green or red light (Zrenner & Gouras 1981), bearing in mind that primates may be important dispersers of the seeds from such fruit. However, care should be taken in generalizing because of important specific differences in colour vision systems, particularly in the UV (Neumeyer 1991; Jacobs 1992; Bennett et al. 1994; Goldsmith 1994; Tovée 1995). Evidence does not fully support the hypothesis that fruit colour increases conspicuousness in particular light environments, and several other hypotheses could explain the evolution of fruit colour (review in Willson & Whelan 1990). Interpretation of the UV-reflectant signals should also be done with great care, since for example UV-reflectant waxy bloom of fruit does not appear to increase detectability by UV-sensitive frugivores (Willson & Whelan 1989), but may in fact have a photoprotection role. Studies conducted on the relationship between colour vision systems and specific plant colour signals concluded that visual systems optimize discrimination of green leaves by dichromatic mammals (Lythgoe & Partridge 1989), the discrimination of flowers by hymenopterans (Chittka & Menzel 1992), and the detection of fruit by primates (Osorio & Vorobyev 1996; Regan et al. 1996, 1998). In terrestrial vertebrates, visual systems also optimize detection of objects against a background dominated by green radiance (Fleishman et al. 1997). As a consequence of distribution patterns of polarized light in forest, various functions of polarized vision (e.g., navigation) must be limited to open areas or to the canopy, whereas other functions can be used even under canopy cover (e.g., determination of surface orientation; object detection – Shashar et al. 1998).

Few studies have investigated the effects and use of light environments in tropical forest animals. Endler (1987, 1991) showed that guppies (*Poecilia reticulata*), small fishes that live in tropical rain forest streams, mostly display during twilight, and that predation takes place in all other light environments. Gup-

pies have highest colour and brightness contrast when they display in purple light at dawn and dusk, and lowest contrasts in the other light environments, especially forest shade. This increases conspicuousness of males to females during courtship, and decreases visibility to predators at other times and places. This variation of conspicuousness with light environments is further increased by the differences in colour vision between guppies and their predators. In anoline lizards of Puerto Rico, Fleishman et al. (1993) showed that UV patterns used for display are only present in canopy species benefiting from high UV levels in ambient light, these signals contrasting with the green vegetation that reflects little UV. Both this study of lizards and that of Marchetti (1993) on birds support the idea that light availability influences habitat selection and species divergence. The influence of light on bird courtship display was studied in lek-breeding manakins and in the cock-of-the-rock (Théry 1987, 1990a, b; Théry & Vehrencamp 1995; Endler & Théry 1996). These birds maximise their conspicuousness to mates, and minimise their conspicuousness to predators, by selecting light habitats in times and places that generate these differences in conspicuousness (Endler & Théry 1996). Each species optimizes its visibility by different combinations of display postures, colours and light habitats (Théry 1990a; Endler & Théry 1996). Among the bird species studied by Endler & Théry (1996), males of any one species use either brightness or colour contrast, but not both. In five sympatric species of lekking manakins, the disposition of colour patches on upper- or underparts can be explained by display height and light incidence in relation to vegetation geometry (Théry 1990a). In the white-throated manakin, light properties of the display site and attendance of the male determine the attractiveness of male display to females (Théry & Vehrencamp 1995). As in guppies, colour and/or brightness contrast is highest at times and places of courtship display to females, and colours are used for mate choice. Another example of the use of light habitats is given by the variation of web colour in *Nephila clavipes*, a large orb-spinning spider widely distributed throughout the New World tropics and subtropics (Craig et al. 1996). Yellow is very attractive to herbivorous and pollinating insects, and this spider attracts and intercepts more insects by constructing webs with yellow pigments (which appear golden in high light intensity). The web colour is adapted to differences of both light intensity and quality, and spiders can adjust pigment production to produce golden webs in a va-

riety of ambient light spectra. In contrast to guppies and lekking birds, which select particular light habitats for specific colour display, this spider adapts its colour signal to a wide range of light environments. In that sense, it is potentially less sensitive to changes of light environment (Endler 1997), which may explain its very wide distribution in forested, edge, and non-forested habitats. Light-environment specialists will, in contrast, show greater sensitivity to modifications of their preferred light environment.

Alteration of light by deforestation, and consequences for biodiversity

Because logging alters the fraction of the sky illuminating objects within the forest (Endler 1997), it also alters the relative abundance of light environments. As disturbance and sky fraction increase, the frequency of woodland shade and large gaps increases at the expense of forest shade and small gaps. As the number and diversity of light environments decrease with the intensity of disturbance, the measurements of light spectra may therefore provide an estimate of the structural impact of forest exploitation (Endler 1997). Because forest light spectra can directly affect animal and plant reproduction and growth, its measurement may also provide a functional explanation of anthropogenic effects on tropical forest diversity. To test this hypothesis, a recent study measured ambient light spectra as well as carrying out a census of manakin birds (Pipridae) and melastome plants (Melastomataceae) (both which are known to have precise light-environment requirements). Irradiance was measured as in Figure 1, and its variation sampled in circles 20 m in diameter. A total of 34 circles were sampled at three sites in primary and disturbed rain forests with similar climate, dominant plant families and bird communities. The gradient of forest disturbance ranged from totally undisturbed forest to different levels of selective logging, an old clear-cut and an active quarry. The ranges of spectral parameters (hue, chroma, total brightness and red/far-red ratio) were measured and analysed in the expectation that sites with more variation in light could support more species which are light-environment specialists.

Positive correlations were found between hue range and manakin diversity, and between the range of red/far-red ratio and melastome diversity (Théry & Endler unpublished). There was no significant relationship between species numbers and means of hue,

chroma, total brightness or red/far-red ratio, and with the ranges of chroma or brightness. There was no significant correlation between manakins and melastomes species numbers. The positive correlations are both an indicator of general habitat loss through anthropogenic disturbance and a direct measure of habitat requirements. However, changes in light environment also correlate with important changes in temperature, humidity and physical structure. It will take controlled experiments to show that change of light habitat itself is the causal factor. Nevertheless, the restriction of light habitats through alteration of forest shade leads directly to the expansion of few high-light demanding species, and to a loss in biodiversity through the disappearance of numerous forest shade or small gap specialists. Melastome fruit constitutes a large proportion of the diet of manakins, which in turn are major dispersers of melastome seeds (review in Krijger et al. 1997), and so these results may not only reflect habitat specialization in manakins and melastomes, but also a direct ecological linkage between the two. Changes in forest light quality may affect each group directly (e.g., melastome germination and development, crypsis and conspicuousness of manakins) or indirectly (e.g., interruption of breeding due to fruit scarcity, inefficient detection of fruit in altered visual conditions). Synergistic effects induced by pollination or seed-dispersal mutualisms are expected to multiply the consequences of light disturbance, and finally to lead to elimination from logged forest (Théry & Endler unpubl. data). This study of effects of human disturbance on forest light and species diversity shows that it is crucial to investigate the use, distribution and importance of light environments in conservation projects.

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