



Review

The effects of preferred natural stimuli on humans' affective states, physiological stress and mental health, and the potential implications for well-being in captive animals



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ARTICLE INFO

Keywords:

Natural stimuli
Sensory needs
Affective states
Well-being
Anxiety
Depression
Stress
Evolutionary signals
Processing fluency
Innate

ABSTRACT

Exposure to certain natural stimuli improves people's moods, reduces stress, enhances stress resilience, and promotes mental and physical health. Laboratory studies and real estate prices also reveal that humans prefer environments containing a broad range of natural stimuli. Potential mediators of these outcomes include: 1) therapeutic effects of specific natural products; 2) positive affective responses to stimuli that signalled safety and resources to our evolutionary ancestors; 3) attraction to environments that satisfy innate needs to explore and understand; and 4) ease of sensory processing, due to the stimuli's "evolutionary familiarity" and/or their fractal, self-repeating properties. These processes, and the benefits humans gain from natural stimuli, seem to be largely innate. They thus have strong implications for other species (including laboratory, farm and zoo animals living in environments devoid of natural stimuli), suggesting that they too may have nature-related "sensory needs". By promoting positive affect and stress resilience, preferred natural stimuli (including views, sounds and odours) could therefore potentially provide effective and efficient ways to improve captive animal well-being.

1. Introduction

There is a pleasure in the pathless woods,
There is a rapture on the lonely shore,
There is society, where none intrudes,
By the deep sea, and music in its roar:
I love not man the less, but Nature more

by Lord Byron, from *Childe Harold, Canto iv, Verse 178*

This review collates an extensive research literature on humans in order to evaluate whether certain natural stimuli have qualities that could benefit animal welfare. We define "natural" as anything that is non-anthropogenic, including natural landscapes, water bodies, sunlight, plants and other animals (Selhub and Logan, 2012). Our view of animal welfare focuses on well-being (cf. Duncan, 2005; Mason and Mendl, 1993), such that natural stimuli would only be considered beneficial if they have measurable, positive influences on animals' affective states. Therefore, we do not consider "natural" to necessarily mean good: after all, considerable suffering probably occurs in animals' natural habitats, and some natural stimuli are highly aversive (cf. the

fear of snakes found in many laboratory primates (Mineka and Öhman, 2002; Van Le et al., 2013) and laboratory rats' innate fear of predator odours (Dielenberg and McGregor, 2001)). But here we argue that data from humans convincingly show that certain preferred natural stimuli can enhance well-being. As a result, even though artificial captive environments can protect animals from natural harms like starvation and predation, our thesis is that they may also deprive of animals of beneficial naturalistic sensory stimulation. Providing preferred, species-relevant natural stimuli, via views, odours, sounds and enrichments, may therefore represent effective ways to improve animal welfare. This would be a new development: animal welfare scientists have not yet investigated the specific welfare benefits of natural stimuli in any formal, well-controlled way, despite the widespread intuition that natural environments have welfare advantages for animals (Fraser, 2008).

To evaluate whether this might indeed be a fruitful avenue for future research, we synthesize a large body of research on the one species that has been very well studied – humans – to review the effects of natural stimuli on the choices people make, as well as the effects of preferred natural stimuli on self-reported subjective states (e.g. moods), affective disorders, physiological stress and even physical health. We also review research focusing on the mechanisms mediating such

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effects. To limit the scope of this review and keep its focus relevant and strongly-evidence-based, we exclude research on the effects of contact with animals where the benefits at least partly reflect social companionship (e.g. pet ownership [Levine et al., 2013], and animal assisted therapy [Nimer and Lundahl, 2007]). We also exclude case studies and therapeutic interventions that do not utilize careful experimental controls (e.g. horticultural therapy). The review is organized by theme, as follows: first, we evaluate humans' preferences for certain natural stimuli, such as natural landscapes over built environments; followed by the effects these natural stimuli have on human affective states, physiological stress, and mental and physical health. We assess the evidence that these beneficial effects are independent of learning or culture: essential for assessing the relevance of human findings for other species. Next we review the diverse, specific attributes of natural stimuli that distinguish them from anthropogenic ones, and that make them attractive and beneficial: important information for guiding how we might extrapolate from humans to other species. Our final section reviews the information on these topics currently available for other species. It also suggests some novel future research directions for psychologists interested in the effects on humans; for neuroscientists interested in the underlying mechanisms; and for animal welfare scientists and others interested in improving animal well-being on farms, in laboratories and in zoos.

2. Evidence that humans prefer natural over built environments

Research consistently shows that humans generally like "Nature". For example, economic techniques reveal reliable preferences in terms of the monetary value placed on access to natural stimuli. Studies using "contingent valuation", a survey-based assessment tool that can estimate the value of natural landscapes, show that people consistently state a strong willingness to pay to create or preserve natural landscapes, particularly if these spaces are close to or viewable from their residences (Brefle et al., 1998; del Saz Salazar and Menéndez, 2005). A second method, "hedonic pricing" – an estimation of how different components contribute to the overall market value of real estate – consistently reveals that the presence of vegetation, water bodies and views of natural landscapes all increase real estate prices (Kroll and Cray, 2010). In a review of 25 (mostly American) studies, Crompton (2001) concluded that nearby parkland has a positive effect on home values and stated that a 20% increase was typical for homes directly adjacent to parkland containing trees and other elements of natural habitat. In urban China, proximity to parkland and water bodies increases high-rise residential values by up to 17% and 13% respectively (Jim and Chen, 2006, 2010). Even street trees can have a positive effect, despite not offering recreational opportunities: in Portland (Oregon), these increase house values by approximately 3%, and decrease the length of time a house is on the market (Donovan and Butry, 2010). Window views of green spaces and water bodies are also sought after. In the Netherlands, these are estimated to increase home prices by 6–12%, while views of other buildings can actually decrease values (Luttik, 2000). In urban China, green space views were likewise found to command a 7% premium (Jim and Chen, 2006), while again, street views had a negative impact on prices (Jim and Chen, 2010).

The visual appeal of natural landscapes has been most thoroughly explored using laboratory preference studies. These unanimously show that photographs of natural landscapes are generally preferred over images of built ones (e.g. of many examples: Kaplan et al., 1972; Kardan et al., 2015a; Purcell et al., 1994). Similarly, studies involving simulations, window views and video recordings also demonstrate preferences for natural landscapes over built environments (Hartig and Staats, 2006; Lottrup et al., 2013; van den Berg et al., 2003). Thus, although people can derive pleasure from architectural design and other human artefacts, typically it is less than that derived from nature: indeed there seems to be little overlap between visual preferences for even the most unspectacular natural settings and built environments

(e.g. Kaplan et al., 1972; Wohlwill, 1976; reviewed by Ulrich, 1986). Furthermore, urban scenes are most preferred when they contain natural elements like vegetation and water (e.g. Abkar et al., 2011; Galindo and Rodríguez, 2000; Herzog and Gale, 1996; also reviewed by Ulrich, 1986). Confounding factors that may influence such preferences have also been considered and controlled for. For example, natural scenes are preferred over built environments even when images are presented in greyscale, indicating that colour is not a confound (Valtchanov and Ellard, 2015); and when scene 'complexity' – the number of independently perceived [dissimilar] elements in a scene as defined by Ulrich (1983) – is experimentally controlled for (Kaplan et al., 1972; Wohlwill, 1976).

Research into non-visual modalities is scarcer. Most soundscape preference studies focus on non-preferred stimuli, especially vehicle traffic noise. However, preliminary research shows that certain natural sounds (running water, birdsongs, insect and frog sounds, rustling vegetation, waves and thunderstorms) are preferred to urban soundscapes and technologically produced noises such as vehicle traffic and construction equipment (Carles et al., 1999; Tamura, 2002; Yang and Kang, 2005). Furthermore, preferences for built environments are increased by adding natural sounds like running water and birdsong (Carles et al., 1999; Hedblom et al., 2014). Some anthropogenic sounds, like bells and ship whistles are also preferred, but these are still not rated as highly as the natural sounds, and can also evoke more annoyance (Tamura, 2002). Of course, music can often be rewarding (McDermott, 2012), but this is not always the case: the study by Tamura (2002) found that people were mostly indifferent to music experienced as part of the urban sound environment.

Many natural odours are also consistently judged as pleasant. In a study by Schleidt et al. (1988), Germans and Japanese were asked to recall odours and rate them for pleasantness. The category "Nature" received the highest ratio of pleasant to unpleasant ratings from both groups; higher than the categories "Food and Drink" and "Civilization" (the latter which was predominantly judged as aversive). Plant odours were unvaryingly judged as pleasant in this study, a finding that is consistently replicated, e.g. for the grassy smell of "green odour" (Oka et al., 2008) and numerous flower odours (Weber and Heuberger, 2008). Indeed, floral, sweet and woody odours have been validated as pleasant manipulations in research investigating the neurophysiological bases of odour hedonics (Rolls et al., 2003).

3. Benefits for human mood, mental health, physiological stress and physical health

Over the last 30 years, several empirical approaches have been employed to investigate whether these types of natural stimuli afford any benefits beyond being preferred, and these have yielded much supportive data. Our focus here is on experimental and epidemiological research that utilizes careful controls to rule out likely confounds (e.g. socioeconomic factors, or other treatment effects not due to natural stimuli *per se*). Section 3 first examines the effects that access to or immersion in natural landscapes have on mood; physiological stress (i.e. hypothalamic-pituitary or adrenal-medullary/sympathetic activation); mental health; and then physical health. Next, the effects of more passive, visual exposure to natural environments – via window views, films and photographs – are reviewed, followed by the effects of natural sounds, and then of exposure to individual plants and views of animals (Fig. 1).

3.1. Access to and immersion in natural environments

One recent illustration of the types of affective benefits common in the literature comes from an innovative study using smartphone technology (MacKerron and Mourato, 2013). Over a six month period, more than 20,000 British participants were repeatedly contacted at random times on their phones. A custom phone application recorded their GPS

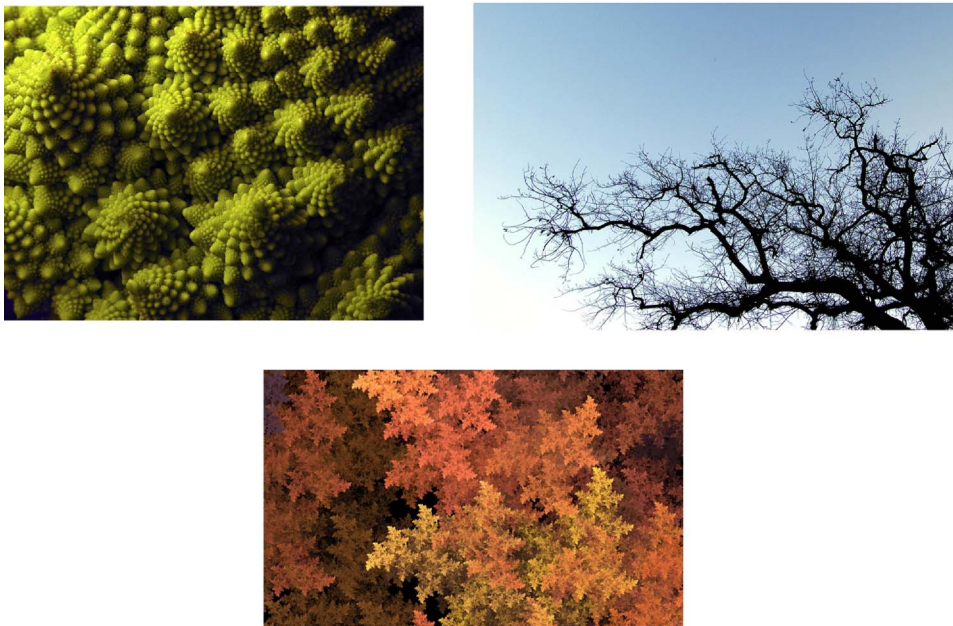


Fig. 1. One quality that distinguishes many natural stimuli is their self-similar, fractal-like patterns such as those seen in trees, river systems, coastlines and mountain ranges. From left to right: Romanesco broccoli (FreelImages.com/Piero Marsiaj); Winter tree (FreelImages.com/René Madariaga); and a computer generated fractal, Autumn leaves (FreelImages.com/Thomas Boulvin), made by continuously looping a pattern at progressively smaller scales.

coordinates, yielding precise data on the environmental conditions at their location, while they were asked to report on their subjective well-being. Participants were also required to answer control questions, e.g. whom they were with and what they were doing, so allowing researchers to tease apart the effects of being in nature from other factors, including whether they were enjoying leisure time or at work. This methodology, which had the advantage of a within-subjects design, revealed that people were happier when they were outdoors in a wide variety of natural environments, compared to when they were outdoors in urban environments – although it was impossible to rule out reverse causality (e.g. people who are unhappy may be less likely to go out and experience natural environments).

This intriguing study complements several larger bodies of work focussing on the affective benefits of living in proximity to nature; of spending time in Japanese forests; and of the environments in which people exercise. Thus, after controlling for socioeconomic status, American children scored as having high levels of nature surrounding their homes were found to be more resilient to stressful events, based on self-report questionnaires administered to both the children and their mothers (Wells and Evans, 2003). Similarly, proximity to green space is associated with lower self-reported psychological stress for people living in deprived neighbourhoods (i.e. with low socioeconomic status and high crime levels): beneficial effects that were found to be independent of physical activity and income (Thompson et al., 2012). These findings are corroborated by a subsequent large scale Danish survey which similarly found an association between green space proximity and decreased self-reported feelings of stress, independent of employment, education and other socioeconomic variables (which were all controlled for in the regression model; Stigsdotter et al., 2010).

This type of long-term exposure to green space (e.g. true wilderness or parks and gardens) also has consistent clinically-relevant effects related to mental health. For example, in Holland, epidemiological data from over 300,000 people have revealed a negative relationship between anxiety and depression prevalence and the amount of green space within a 1-km radius of people's homes, particularly for children and people with lower socioeconomic status (Maas et al., 2009). Proximity to green space is also associated with decreased symptoms of anxiety and depression in the United States (Beyer et al., 2014) and decreased anxiety and mood disorders in New Zealand (Nutsford et al., 2013). Vegetation (especially trees) likely contributes to these benefits. Even after controlling for socioeconomic status, anti-depressant

prescription rates were found to be lower for London residents exposed to a greater density of street trees (which ranged from 15.7/km to 81.7/km): with each additional tree per km, 0.1% fewer prescriptions were written (Taylor et al., 2015).

Controlled or cross-over studies investigating whether exercising in nature provides additional benefits over exercising in non-natural environments have recently been systematically reviewed by Coon et al. (2011), who synthesized 11 experiments comparing exercise in nature to exercise indoors, and by Bowler et al. (2010), who reviewed 25 studies comparing exercise in nature to exercise either indoors or outdoors in built environments. These found that exercising in natural environments *does* provide additional improvements to self-reported emotional well-being, including increased enjoyment and reduced feelings of tension, anger and depressed mood. Additionally, Bratman et al. (2015) found that walking in natural compared to built environments reduced subjects' tendencies to ruminate on negative thoughts, findings consistent with electroencephalography data suggesting that compared to built environments, exercising in nature promotes meditative-like mental states (Aspinall et al., 2013). Finally, a recent meta-analysis of 32 randomized, controlled studies measuring the mood effects caused by exposure to natural scenery found robust effects on self-reported emotional state, including moderate increases in positive affect and, to a lesser extent, decreases in negative affect (McMahan and Estes, 2015). Although green space is the most common type of nature exposure in these studies, other natural features besides vegetation seem to produce even greater effects. A recent meta-analysis based on 10 studies conducted at the University of Essex revealed that mood improvements experienced in outdoor vegetated areas were greatest when those green spaces were bordered by water (Barton and Pretty, 2010). Likewise, based on over one million responses (using the previously mentioned smartphone app), MacKerron and Mourato (2013) also found that coastal areas were the locations where people were happiest.

In the 1980's, the Forest Agency of Japan began to promote the perceived benefits of "forest bathing" – essentially time spent walking in and observing forests – and considerable attention has since been given to this topic by Japanese researchers. Consistent with the studies described above, spending time in the forest improved subjects' self-reported moods (Lee et al., 2009; Lee et al., 2011; Park et al., 2011; Park et al., 2010; Song et al., 2015; Tsunetsugu et al., 2013). Importantly, these data were complemented by measures of physiological

stress and immunological function. Thus in one example, subjects participated in walking excursions in forests and outdoor urban environments: either visiting three different forest locations; or an airport, a baseball stadium and a historical tourist district in Nagoya, Japan. Subjects' activity levels were matched (two to four hours of walking per day) and blood and urine samples were taken to provide measurements of both baseline adrenaline, and natural killer cell numbers and activity levels. The forest, but not the city, increased natural killer cell measures for a minimum of seven days, while also decreasing urinary adrenaline (Li et al., 2008b; see also Li et al., 2007 and Li et al., 2008c). Similar experiments utilizing within-subject designs also found marked physiological benefits from spending time in forests compared to urban areas, including increased parasympathetic activity and reduced sympathetic activity (both assessed via heart rate variability); and reduced salivary cortisol, heart rate and blood pressure (Lee et al., 2011, 2009; Park et al., 2010, 2008; Song et al., 2015).

Despite a large diversity in testing locations and impressive efforts to control confounds, not every factor was held equal in these Japanese studies however: for example, forest environments were often cooler and more humid than the urban environments, which sometimes neared 30 ° Celsius (Lee et al., 2009; Song et al., 2015); and in order for researchers to obtain ethical approval, their subjects were notified of the study objectives, and so were not blind to the hypothesis. Furthermore, not all types of natural environments have been found to reduce physiological stress. The many studies comparing exercising in natural environments (primarily public parks and college campuses) to exercising indoors (as reviewed Coon et al., 2011) or to exercising outdoors in built environments (as reviewed Bowler et al., 2010) have not generated conclusive evidence that the former reduces cortisol, blood pressure, or other signs of physiological stress.

In contrast, research consistently shows that living in areas with vegetation and natural views can have physical as well as mental benefits. Thus in the Netherlands, proximity to green space improves self-reported general health independent of socioeconomic and demographic factors (Maas et al., 2006; van den Berg et al., 2010). In Canada, neighbourhood street trees are also reliably associated with improved self-reported health for Toronto residents, with more trees predicting better physical health, independent of income, education and age (Kardan et al., 2015b). For example, an additional 11 neighbourhood street trees per city block measurably reduced residents' risk of cardiovascular disease, and to the same extent as a \$20,000 income increase (Kardan et al., 2015b). Such effects can even influence mortality rates. In Japan, access to walkable green space is associated with improved survival in elderly residents (Takano et al., 2002), while residential proximity to forests negatively correlates with cancer mortality rates, even after controlling for smoking and socioeconomic factors (Li et al., 2008a). Green space proximity was also found to reduce income related health inequalities in England, resulting in less cardiovascular and all-cause mortality in economically deprived neighbourhoods (Mitchell and Popham, 2008), findings since replicated in Canada (Villeneuve et al., 2012) and in another large scale English study (Lachowycz and Jones, 2014). Fascinatingly, although such effects are commonly thought to result from nature's facilitation of exercise, this last study found no evidence that physical activity mediated the effects of green spaces on mortality, suggesting that other factors, including psychological benefits, are important (Lachowycz and Jones, 2014). Finally, the spread of the Emerald ash borer, an insect that has killed over 100 million trees in North America, provides a rare opportunity to test for a causal link between trees and human mortality. After controlling for socioeconomic factors and changes in mortality rates over time, tree loss was found to predict an increase in cardiovascular and respiratory mortality by approximately 24 deaths/100,000 people a year (Donovan et al., 2013). (Note that other effects of outdoor access on aspects of physical functioning, such as eyesight, are covered later in Section 5.4).

3.2. Natural views: mood, stress and health effects of vistas, videos and images

These benefits of reduced stress and improved health and well-being do not require immersion in nature: they have also been observed in people exposed only to window views, television displays and even photographs of natural scenes (with virtual reality technology – still underutilized in public health and environment psychology research [Smith, 2015]– perhaps yielding further data in the future).

In the first pioneering study of this type, Ulrich (1984) reviewed the records of hospital patients recovering from gallbladder surgery. Patients with window views of nature (grass and trees) were compared to those whose views consisted of an adjacent brick wall. After matching for relevant factors (age, sex, lifestyle factors, prior medical history and other room characteristics), and ensuring no systematic biases in medical care, patients with views of nature were found to have required lower doses of analgesics; their nurses wrote fewer negative comments about their mental well-being (e.g. “upset and crying”); and they even had faster average recovery times (7.96 vs 8.70 days). Ulrich was careful to caution that the brick wall view lacked complexity, arguing that views of a busy street, for instance, would have provided better controls; but more recent research utilizing such improved controls does support that a window view of natural scenery is indeed beneficial. For example, workers with forest views from their office windows reported reduced psychological stress and frustration, and greater life satisfaction and physical health, compared to workers with views of built environments (Kaplan, 1993; Sop Shin, 2007). In domestic settings, having views of grass, trees or water also improved self-reported measures of neighbourhood satisfaction and well-being when American residents were compared within the same apartment complexes (Kaplan, 2001).

Viewing nature videos can also reduce physiological stress and improve mood. After viewing a stress-inducing video about workplace accidents, subjects were exposed to videos of either nature (forest, running water) or urban scenes (traffic, pedestrians). Physiological stress recovery was faster and more complete (compared to baseline levels) in the nature treatment, assessed via skin conductance and blood pressure, as well as lower muscle tension (Ulrich et al., 1991). In a similar study, participants viewing simulated car rides through natural scenery had reduced blood pressure and skin conductance following a stressor (an unsettling film or attention demanding task), compared to participants who viewed a simulated car ride through a built environment. Increased smiling (assessed using facial electromyographic activity in the cheek region) during the nature simulation also suggested improved affective state (Parsons et al., 1998). Likewise, after performing a mentally demanding task, subjects who viewed a “virtual tour” of a western Norwegian coastal area had reduced heart rate compared to subjects who viewed a tour of downtown Oslo (controlling for baseline heart rate) (Laumann et al., 2003).

Other studies have found that even viewing photographs of natural scenery can reduce physiological stress. In research conducted at NASA's Ames research centre, galvanic skin conductance (an indicator of sympathetic activation) was lower following a mental stressor if subjects were exposed to natural imagery compared to a non-natural pattern or a blank canvas (Wise and Rosenberg, 1986, cited in Wise and Taylor, 2002). In other experiments, viewing nature photographs increased baseline heart rate variability (suggesting reduced sympathetic activity) as well as that seen after recovery from a mentally demanding task (Brown et al., 2013; Gladwell et al., 2012). This idea of reduced stress is supported by functional MRI (fMRI) research showing that the presentation of urban images (including some unpleasant scenes) significantly increased activation in the amygdala, while presenting rural images instead significantly increased activation in the basal ganglia (Kim et al., 2010a, 2010b). The mere presence of angular edges in built scenes may explain some of these effects: another study found that sharp edged objects also increased amygdala activation compared to

equivalent round edged objects (Bar and Neta, 2007), which these authors hypothesise is due to sharp objects signalling a threat (Bar and Neta, 2006).

3.3. Effects of exposure to natural soundscapes and odours

Research into the stress-reducing effects of natural sounds has not consistently produced significant results when loudness is properly controlled for. For example, listening to natural sounds (bird songs and running water) did not significantly reduce skin conductance, and failed to increase heart rate variability following a mentally demanding task, compared to listening to traffic noises (Alvarsson et al., 2010). However, other similar studies have found that natural sounds *can* have stress reducing effects (albeit not on all variables: heart rate and blood pressure were unaffected, for example, in the two studies that follow). Thus in subjects required to give a psychologically stressful oral presentation, heart rate variability during the recovery period showed greater increases (compared to baseline) when they were exposed to a virtual nature experience that included congruent sounds (birds, a babbling brook) compared to one presented in silence (Annerstedt et al., 2013). Likewise, surgery patients who listened to rustling leaves and bird songs during surgery (compared to regular operating room sounds) had lower salivary alpha-amylase levels, a biomarker of decreased sympathetic activity (Arai et al., 2008). Turning to natural odours, plant scents have been found to improve mood (e.g. Weber and Heuberger, 2008) and to reduce physiological stress (e.g. Fukada et al., 2012). Whether these effects are mediated by sensory versus direct physiological routes is unclear, so this topic will be covered in Section 5 which explains why certain natural stimuli may be beneficial.

3.4. Effects of exposure to animals and indoor plants

Indoor plants do not always have significant beneficial effects on mood and physiological parameters, but one consistent result is that they help mitigate the subjective experience of pain (reviewed in Bringslimark et al., 2009). In one example of a well-controlled study, people were willing to submerge their hands in ice cold water for a longer duration in a room containing plants, compared to in a room containing inanimate objects that were rated equally interesting (Lohr and Pearson-Mims, 2000) – an effect that can be mimicked, as we will see in Section 5, by just the smell of plants. When handed out to strangers, individual flowers have also been experimentally shown to improve affective state and elicit positive social behaviour to a greater extent than human made artefacts (a pen with a university logo) (Haviland-Jones et al., 2005).

Can animal stimuli be similarly beneficial? The benefits of pet ownership and animal assisted therapy are well documented (e.g. Levine et al., 2013; Nimer and Lundahl, 2007), although typically dog-focused and ascribed to social bonding effects rather than to the close proximity

of other life forms (thus beyond the focus this review). In contrast, there have been few controlled experiments on the effects of more passive exposure to animals. Holcomb et al. (1997) found that adding an aviary to the common room of a medical facility reduced self-reported depression in elderly patients. However, they failed to include an interesting, non-animal control, so that other explanations like novelty or increased interactions between patients cannot be ruled out. Placing an aquarium in a dementia hospital also reduced the amount of “uncooperative, irrational and inappropriate” behaviour performed by patients, but again, this study compared treatment effects to baseline behaviour and did not use a novel control (Edwards et al., 2014). Two better-controlled studies looked at variables other than self-reported affect. In one aimed at alleviating unhealthy levels of weight loss in Alzheimer patients, Edwards and Beck (2002) determined that adding an aquarium in a hospital dining room resulted in greater nutritional intake compared to when a scenic ocean photograph was placed in the room. The aquarium seemed to capture patients’ attention, causing them to remain seated for longer durations. Another found no difference in heart rate and muscle tension from viewing an aquarium compared to a placebo (a video falsely claiming to contain relaxing subliminal messages) following a cognitive stressor, but this experiment had limited power due to small sample sizes (DeSchrive and Riddick, 1990).

Finally, videos of animals may have beneficial effects. Online cat videos have reached more than 26 billion views worldwide (Marshall, 2014, cited in Myrick, 2015). A recent survey completed by nearly 7000 users of this content (admittedly self-selected) found that cat videos provided an effective means to both increase positive affect and decrease negative affect (Myrick, 2015). The emotional benefits even outweighed the guilt associated with procrastination, suggesting that this media is sought out as a form of “digital pet therapy”. Turning to physiological effects, viewing videotapes of fish, birds or primates was found to more effectively reduce blood pressure and heart rate following a cognitive stressor, than viewing a soap opera or a blank screen (Wells, 2005).

3.5. Summary

Some of the reviewed literature does have limitations, as we have seen. Considered as a whole, it also leaves unanswered some key questions about why the magnitude of measured benefits varies across studies, and whether the extent to which natural stimuli are preferred determines the magnitude of their effects on mood, physiological stress and health (all questions that suggest this field may now be ripe for meta-analysis). Overall, however, the research strongly supports the hypothesis that exposure to certain types of natural stimuli (or even videos or images of them) can improve health and well-being, and reduce stress and negative affect, more than anthropogenic stimuli of similar interest or complexity. The key results are summarised in Table 1.

Table 1

Key results from humans on the potentially beneficial effects of natural stimuli (independent of potential confounds like socio-economic status and levels of exercise).

Effect	Strongest evidence
Meeting people's preferences	Effects of bodies of water, vegetation and views of nature on house prices Laboratory preference studies involving still and moving images, natural sounds, and plant odours
Enhancing mood and reducing self-reported subjective stress	Long-term effects of proximity to green space (e.g. ready access from home) Immediate effects of immersion in natural landscapes (e.g. via taking walks) Immediate effects of viewing natural vistas in images or videos, or via windows Immediate effects of plant odours
Reducing physiological stress responses	Laboratory studies of effects of videos and still images of natural views Laboratory studies of effects of some natural sounds, odours and animal videos
Improving health	Effects of access to trees and green spaces on cardiovascular disease and depression Effects of window views of nature on hospital recovery times Effects of outdoor access on myopia (see Section 5.4)

Importantly, the research presented in this section spans diverse nationalities and cultures, suggesting that in humans, the beneficial effects of natural stimuli may be universal. Next we therefore assess in more detail whether such effects, as well as the preferences engendered by attractive natural stimuli, are best explained by innate or by experiential, culture-related processes.

4. Are these beneficial effects on humans innate or cultural?

The role of culture and experience in peoples' positive responses to nature is not fully resolved. These issues are important because if they completely account for the benefits of natural stimuli, then human data may have no relevance beyond our own species. Some evidence does show that experience with nature, especially in childhood, increases both positive attitudes towards nature (Lohr and Pearson-Mims, 2005; Zhang et al., 2014) and the benefits derived from nature later in life (Mayer et al., 2009). It is not known, in contrast, whether exposure to natural stimuli during development is *necessary* to elicit these later benefits. Most authors, however, believe not: innate factors are typically assumed to at least partially explain nature's benefits. This idea was popularized in E. O. Wilson's book "Biophilia" (1984), which argued that humans have instinctive attractions to other forms of life. Various types of evidence provide support, as we review next. These include research into primary reinforcers; cognitive findings in infants; the seemingly involuntary nature of many of the effects; and an apparent lack of cultural specificity.

The first type of supporting evidence is the most indirect, and concerns the fundamentals of primary reinforcers. A number of stimuli elicit approach or avoidance, and condition learned responses, without prior experience of their biological consequences. Humans' innate preferences for sweet flavours are one example (Ventura and Mennella, 2011). Some odours, including sweet and flowery smells are likewise inherently pleasant (Joussain et al., 2011; Kermen et al., 2011; Khan et al., 2007; Mandairon et al., 2009; Poncelet et al., 2010), as are certain tactile stimuli (e.g. gentle strokes; Taira and Rolls, 1996). Positive primary reinforcers are argued to be so reliably associated with fitness that it is adaptive for infants to enter the world "pre-programmed" to find these stimuli attractive (Rolls, 1999; Ventura and Mennella, 2011). Some natural stimuli act as primary *negative* reinforcers, in contrast, motivating avoidance. Again, these seem to be reliable as signals of harm, and include vomit, putrefaction and other signals of disease (e.g. Rolls, 1999), and "biophobias": fearful responses to certain organisms (e.g., snakes and spiders) (Lichtenstein and Annas, 2000; Mineka and Öhman, 2002; Rolls, 1999). Since preferences and aversions for stimuli important to evolutionary fitness can be innate rather than learned, this has been used to argue that positive responses to certain landscapes and other natural stimuli are similarly innate (Lohr, 2007; Orians and Heerwagen, 1992; Ulrich, 1993), evolving in our ancestors because of their value for fitness (an idea we return to in Section 5).

The second type of evidence for innateness comes from studies of babies and infants. New-born infants perceive some natural and non-natural stimuli differently, for instance preferentially attending to "animate" motion over non-animate (Bardi et al., 2011; Bidet-Ildei et al., 2014; Simion et al., 2008). This has been tested by sparsely placing point lights on objects or the bodies of animals in digitized videos, so that subjects can only view the movement patterns made by these lights. Animal movement, characterized by a mixture of rigid and non-rigid motion, attracted more visual inspection than similar point light displays from, e.g. rotating rigid objects (Bardi et al., 2011), suggesting that human neonates are innately predisposed to attend to animal motion (Bardi et al., 2011; Simion et al., 2008; Troje and Westhoff, 2006). Infants are also able to discriminate unfamiliar stimuli with natural acoustical structure from unfamiliar artificial stimuli (Gervain et al., 2014), and young children tend to spontaneously categorize natural from human made stimuli (Wohlwill, 1983). Infant humans thus seem to find natural and anthropogenic stimuli

intrinsically distinguishable, without being taught.

The third line of evidence for innate biophilias is that they and the processes involved often seem implicit, i.e. not mediated by conscious awareness. Thus attendance to certain natural stimuli is often involuntary. For example, in rapid object detection tasks, people's eye saccades automatically move towards images of animals, even when they are aiming to target inanimate objects (Crouzet et al., 2012). Similarly, evidence suggests that rapid visual preference judgements for natural scenery rely on automatic "bottom-up" processing that is driven by low-level visual features (particularly spatial and colour properties) (Kardan et al., 2015a). Thus, rapid preference judgements for natural scenery can be made independently of contextual information like conscious understanding of the content (Kardan et al., 2015a). Consistent with this, people often have difficulty describing the physical factors that underlie their visual preferences for natural environments (Kaplan, 1992; Redies, 2007); which also seem immune to information interventions intended to manipulate aesthetic preferences (Hill and Daniel, 2007). It has even been found that people are not fully aware of the mood benefits they experience from exercising in nature. These typically exceed what people predict they will experience, and this under-prediction does not occur for exercise in built environments (Nisbet and Zelenski, 2011). It remains possible that these effects have been made implicit thorough repetitive conditioning; however, pending further research into mechanisms, these findings suggest the involvement of innate processes rather than culturally developed tastes that should be more voluntary, malleable and easier to articulate.

Finally, if learned factors did account for nature preferences, one would expect wide variation between cultures, but this is not the case: visual preferences for natural over built environments are widespread globally. Studies involving diverse cultures consistently find that people prefer their local natural environments to their local built environments, or that they prefer their built environments to contain natural features e.g. in South and North Europe, and North America (Galindo and Rodríguez, 2000; Purcell et al., 2001; Staats et al., 2003; Ulrich, 1986); Asia (Abkar et al., 2011); Australia (Purcell et al., 1994); and Africa (Chokor and Mene, 1992). Moreover, a meta-analysis including 40 cross-cultural comparisons found that demographic factors only play a marginal role in visual landscape preferences (Stamps, 1999). In one study, objective image descriptors accounted for up to 40% of the variance in American and Korean's landscape preferences, whereas culture, occupation and semantic knowledge (e.g. whether the image depicted a location of cultural significance) together accounted for less than 10% (Yi, 1992, cited in Parsons and Daniel 2002). Lastly, research involving culturally diverse children – urban African Americans, Brazilians from urban and remote rural locations, and urban Portuguese – all finds that natural environments are preferred and valued (Kahn, 1997; Kahn et al., 2009). Kahn (2002) proposes "universal features in children's environmental conceptions and values" that persist even when children are raised in degraded or destroyed ecosystems (e.g. polluted inner city Houston).

Overall, culture and experience thus cannot fully explain humans' positive responses to natural stimuli. Many researchers therefore argue that innate processes are involved, perhaps evolving because the rapid processing of and/or instinctive attraction to certain stimuli was beneficial to our ancestors' fitness. This makes it plausible that biophilias are not unique to humans, but instead present in other species. We revisit this idea and its implications in Section 6, but first we review what is known about the specific properties of attractive, beneficial natural stimuli: what makes them effective? Parsing out effective attributes in this way could help reveal what types of stimuli might be similarly beneficial for other species.

5. What makes certain natural stimuli attractive and beneficial?

As we have reviewed, certain natural stimuli or environments are often preferred and provide health and well-being benefits. Their

specific properties and how they differ from anthropogenic stimuli is less well researched; however, it is a fascinating and growing area, and one crucial to understand to develop principles relevant to other species. This section therefore reviews the diverse features that both distinguish natural stimuli or environments from artificial ones, and potentially explain their benefits. To do this, first we review effects of some specific individual components of exposure to nature: sunlight, negative ions, certain plant compounds, and beneficial bacteria. We then discuss the idea that humans have evolved to find certain natural scenes attractive because evolutionarily they signalled safety or resources. Next we consider some broader properties of preferred natural scenes, such as their degree of complexity. Finally, we look at how “perceptual fit” and processing ease influence humans’ preferences. This last section will discuss stimulus properties that our sensory organs are adapted to, including evidence that humans have evolved predispositions for processing information about stimuli historically important for fitness.

5.1. Specific natural products and stimuli that are beneficial

Natural light exposure can be intrinsically important, and is thus one specific contributor to the beneficial effects of nature. For example, direct exposure to sunlight has long been known to be crucial for Vitamin D synthesis (Webb, 2006) which improves bone health and may protect against certain cancers and autoimmune diseases (Holick, 2004). However, even sunlight largely stripped of ultraviolet-B radiation (the wavelengths responsible for these effects) may be beneficial. For example, Walch et al. (2005) determined that spinal surgery patients randomly assigned to rooms with greater sun exposure reported lower perceived stress and used less analgesic medication, suggesting they were less troubled by pain. Similarly, in a retrospective study, psychiatric patients with clinical depression (assumed to have been randomly assigned to rooms), were discharged sooner if kept in sunny rather than dull rooms (Beauchemin and Hays, 1996). In both studies, however, the potential confound of window view content was not addressed, and so it cannot be confirmed that sunlight alone was the critical factor. Natural lighting may have health advantages over artificial lighting because it is free from flicker, which has been shown to cause headaches in brightly lit workplaces (Wilkins et al., 1989). With fluorescent lighting, this problem can be alleviated using higher frequency ballasts (Wilkins et al., 1989), however, even high frequency flicker rates unperceivable to humans may cause headaches, eyestrain and decreased visual performance (Bilić and Cifrek, 2015).

Air quality and odour may also play an important role. Air in urban and indoor settings typically contains higher levels of toxins and other contaminants (Tsao et al., 2014), and ventilation has marked effects on indoor air quality, with greater outdoor air intakes improving the health and comfort of building occupants (Burge et al., 1987; Mendell et al., 1996; Milton et al., 2000; see also Section 5.4). However, even well-ventilated buildings are at a disadvantage against open natural environments, which allow airborne pathogens and other contaminants to disperse via wind and diffusion; and contain vegetation which removes some airborne contaminants (Dela Cruz et al., 2014) and produces oxygen and other beneficial airborne chemicals. These include aromatic, antimicrobial chemicals called phytoncides, which occur in much higher concentrations in forest air compared to urban environments (Li et al., 2008b). Phytoncides from coniferous trees have been found to increase humans’ natural killer cell activity if vaporized into indoor environments – mimicking a known benefit of immersion in forested environments (Li et al., 2009). Other aromatic plants, including rosemary, lavender, rose and chamomile (which contain some of the same volatile compounds as conifers) can reduce physiological stress and improve mood in humans (e.g. Fukada et al., 2012; Moss et al., 2003; Williams, 1992). Additionally, leaf aldehydes and alcohols, generally referred to as “green odours”, are widely considered to be pleasant smelling (Oka et al., 2008; Spiers et al., 2015) and evidence is

mounting that these compounds also have stress reducing properties. For example, smelling a mixture of 2E-hexenal (leaf aldehyde) and 3Z-hexenol (leaf alcohol) reduced the blood pressure of subjects submerging their hands in iced water (Oka et al., 2008) and increased the pain thresholds of people exposed to mechanical forces (Aou et al., 2005). Vegetation also replenishes negative air ions (Wang and Li, 2009) which, according to a recent meta-analysis, may alleviate depression at high exposure levels, although no immediate mood benefits of negative ion therapy were found (Perez et al., 2013). Negative air ions are also replenished by atmospheric radiation (Wang and Li, 2009; Yamada et al., 2009) and rapidly flowing water (Kolarz et al., 2012) and are thus found at higher concentrations in rural areas compared to urban or indoor environments (Hawkins, 1981; Liang et al., 2014).

Aside from airborne molecules, numerous other substances could provide health and mood benefits, especially for children, whose exposure to these substances is likely increased by their exploration and play. For example, one common strain of soil bacteria *Mycobacterium vaccae* is thought to directly improve mood by elevating serotonin levels (Lowry et al., 2007). Overall, all these items speak to one of the most direct possible explanations for the benefits of natural environments: that they contain specific biologically-active components that have therapeutic benefits.

5.2. Evolutionary signals of safety and plenitude

Certain specific natural stimuli or landscapes may be affectively positive primary reinforcers because they were useful evolutionarily, providing cues that once signalled safety or resources. For example, to explain why grassland environments with scattered trees are often preferred over other natural environments (Balling and Falk, 1982; Herzog et al., 2003; Hill and Daniel, 2007), and why preferences for savannah-typical trees are also common (Lohr and Pearson-Mims, 2006; Orians and Heerwagen, 1992; Summit and Sommer, 1999), it has been hypothesized that this is because savannahs were the original ancestral habitat for *Homo erectus*. Savannahs provided the benefits of unrestricted movement, trees for climbing and shelter, and vegetation and animals for utilization as food, with modern-day preferences argued to be a legacy of these benefits (Orians and Heerwagen, 1992). Some authors speculate that human modified landscapes, including ancient pastoral landscapes and manicured parks, which share some of the distinctive features of savannahs, are modelled off this ancestral environment (Falk and Balling, 2010; Parsons and Daniel, 2002).

Although a popular notion, the claim that savannahs were the only ancestral habitat for *Homo erectus* is contested (White et al., 2009). More general “psycho-evolutionary” arguments sidestep this controversy because they are not wedded to one particular phase of our evolutionary history. Instead, they propose more broadly that our widely documented preferences for water bodies, trees and other healthy vegetation (e.g. Han, 2007; Völker and Kistemann, 2011) exist in part because these features would ancestrally have signalled access to water and food (Lohr, 2007; Ulrich, 1983). Humans’ attraction to flowering plants is likewise suggested to reflect their past importance in signalling future sources of fruit and seeds (Haviland-Jones et al., 2005; Rolls, 1999). Elevation changes, climbable trees and open vistas are other commonly preferred features in landscapes. “Prospect-refuge theory” proposes that this reflects innate desires for opportunities to obtain useful information (e.g. to prospect for food, predators and distant weather conditions), while also satisfying needs for privacy and safety in refuges (Appleton, 1975). Ulrich (1986, 1993) argues that these cues can still today cause rapid, automatic positive affective responses, and reduce anxiety and stress, because they ancestrally indicated safety and resources. Conversely, visual preferences for natural environments are decreased when they contain signals of danger such as a stormy sea, threatening humans or predator animals (Ulrich, 1983, 1986), or immersion in dense vegetation that raises concerns about restricted visibility and entrapment (Herzog and Kutzli, 2002).

This type of explanation for preferred natural stimuli is intriguing and plausible, fitting well with the commonly held view that emotional responses serve an adaptive function (Fredrickson, 1998; Mendl et al., 2010; Panksepp, 2005). However, its hypotheses are difficult to test; its validity is debated (Joye and van den Berg, 2011); and it does not account for all properties of beneficial natural environments, as we detail next.

5.3. An informational perspective on environmental preference: complexity and related characteristics

A popular explanation for environmental preferences is that people have evolved needs to understand and explore, and much research has focused on the role of information-based variables like complexity and coherence in predicting scene preferences (Kaplan and Kaplan, 1989). In visual research, preferences for complexity tend to follow an inverted U-shaped curve, with levels that are too low or too high being less preferred (Palmer et al., 2013; Wohlwill, 1968). For scenes of natural and built environments, most studies show that complexity (either subjectively rated or quantified based on colour and spatial properties) is positively associated with preference, suggesting that people are more prone to dislike environments for being monotonous and unstimulating (Kaplan et al., 1972; Kardan et al., 2015a; Schirpke et al., 2013; Stamps, 2004). Preferred visual scenes are often also rated as “coherent”, meaning that they have understandable spatial organization (Abkar et al., 2011; Herzog, 1989). This may involve “redundant elements, textures and structural features” that facilitate “prediction from one portion of the scene to another” (Kaplan and Kaplan, 1989). Thus, preferred environments are argued to be close to an optimal level of complexity, and organized in a way that makes them interesting, without being overwhelming or too challenging to comprehend (Kaplan, 1992). Preferences for intermediate complexity and coherence may be explained by a trade-off between desires to explore and understand: motivations that have evolved because they arguably aid fitness. Kaplan (1992) argues that by being both easy-to-read and offering the promise of readily-available novel information, natural environments encouraged human ancestors to explore and expand their cognitive maps, which provided future advantages when their survival was threatened (e.g. finding escape routes, hiding places, food and water resources).

Evidence that these and other information-based variables (e.g. “prospect-refuge”: Dosen and Ostwald, 2016) are related to visual preferences has been used to argue that people are pre-disposed to make subconscious inferences about the ancestrally useful opportunities supplied by different environments (Kaplan and Kaplan, 1989). This idea is also captured by Gibson’s influential “Theory of Affordances” (Gibson, 1977), which describes environments in terms of the behavioural opportunities they offer (termed “action possibilities”) and argues that “values and meanings of things in the environment can be directly perceived” (Gibson, 2015). Consistent with this, environments self-rated as compatible with individuals’ “purposes or inclinations” are found to be visually preferred (Herzog et al., 2003).

Coherence, complexity and the promise of novel information are characteristics that exist in time as well as space, and natural environments may also be attractive because they are dynamic systems that fluctuate in time, providing incremental variation and diversity. However, while this is empirically supported for short-term fluctuations (Hetherington et al., 1993), there is still a lack of data on the attractiveness of longer-term environmental changes, likely due to numerous challenges with testing this hypothesis in a lab setting (Daniel, 2001). Natural systems also contain a great variety of stimuli that are layered and manipulable, and organized such that learning cues and patterns can allow individuals to understand and exploit their environment more effectively. This includes using indirect cues to predict and facilitate beneficial opportunities (including hunting and foraging). Together, these factors may provide choice, control and opportunities for rewarding exploration that are hard to reproduce in non-natural settings.

5.4. “Perceptual fit” and of ease of processing

Many of the qualities summarised above relate to a concept termed “soft fascination”: a phrase describing how natural stimuli are inherently interesting, yet attract attention rather effortlessly (Herzog et al., 1997; Kaplan, 1995; van den Berg et al., 2007). This “effortlessness” may reflect the ease with which natural stimuli are processed: the topic reviewed next. In the field of neurophysiology, it is widely assumed that sensory systems are optimized for the stimuli that they evolved to process (e.g. Lesica and Grothe, 2008; Reinagel and Laughlin, 2000; Schwartz and Simoncelli, 2001; Simoncelli, 2003). This is relevant in two broad ways: there is evidence that our sensory organs sometimes function less well in anthropogenic than in natural environments, and also that the central processing of stimuli may be faster and less effortful for natural than for artificial stimuli.

Natural environments normally contain stimuli within the physical ranges that our sensory organs evolved to process well. They are thus free from many of the damaging or aversive sensory qualities that can contribute to discomfort in built environments such as cities, factories and farms. Chronic exposure to intense sounds can damage hearing function (Passchier-Vermeer and Passchier, 2000; Sliwiska-Kowalska and Davis, 2012), and this problem can be compounded by acoustically reflective surfaces like metal and concrete (Vorländer, 2007). Aversion to certain anthropogenic sounds is not simply attributed to intensity levels. “Roughness” and “sharpness” are aversive properties of many machine produced noises that are related to wave frequencies and how they interact with ear structures (e.g. frequencies that fall within the resonance range of the ear canal are more aversive and damaging) (McDermott 2012). Thus, machine noises are commonly cited as causes of annoyance, particularly traffic noise: a known cause of sleep disturbance (Pirrerera et al., 2010). The presence of off-gassing materials, combustion exhaust, perfumes and other odorants in built environments can also contribute to olfactory dysfunction (Cone and Shusterman, 1991) and discomfort, including headaches, and eye, nose and throat irritation (Schiffman, 1998). Again, these problems can be compounded by spaces with restricted airflow that trap airborne contaminants (Cone and Shusterman, 1991). Built environments also typically contain unvarying light that is reflected off smooth, monotonous surfaces. In contrast, natural light varies in terms of intensity, colour, and the angles with which it contacts the earth’s surface, and depending on weather conditions it may be experienced as diffused light or direct sunshine (the latter also being a source of radiant heat). These properties also change as light filters through vegetation (Enderler, 1993), providing zones of “dappled” light. Unlike commonly used artificial lights (incandescent, fluorescent and LED), natural light is full spectrum, containing fairly even levels of every wavelength, from the ultraviolet to the infrared ends of the spectrum. Finally, outdoor natural light is typically brighter than indoor artificial lighting (Rose et al., 2008a). Whether any of these properties make natural light beneficial is not firmly established, but there is mounting epidemiological evidence that children who spend more time outdoors have reduced myopia, even after statistically controlling for physical activity and “near-work”, e.g. reading, writing and computer use (Jones et al., 2007; Rose et al., 2008a; Rose et al., 2008b). A recent meta-analysis estimates a 2% reduction in odds for myopia for each additional hour spent outdoors per week (Sherwin et al., 2012).

There is also evidence that humans have evolved to process even complex information from natural environments with relative ease. This seems to arise from two effects: hardwired mechanisms that make us more accurate and efficient at detecting specific natural stimuli (e.g. animals; Crouzet, 2012; New et al., 2007); and more speculatively, the way that the structurally redundant – often “fractal” – properties of natural environments make them easy to process (Cheung and Wells, 2004; Joye and van den Berg, 2011; Kardan et al., 2015a; Purcell et al., 2001).

The strongest direct experimental evidence involves humans' extraordinary abilities to rapidly, accurately detect diverse animals in visual scenes. Thus, in the near absence of attention, humans are able to detect animals in natural scenes with high accuracy, while being unable to perform seemingly less complex tasks when stimuli are artificial (e.g. detecting a randomly rotated letter "T" or "L"; Li et al., 2002). Humans can also detect animals with greater speed and accuracy than they can detect vehicles (Crouzet et al., 2012); and are faster and more accurate at detecting changes in complex scenes when the changes involve animals (human or non-human), compared to when the changes involve inanimate objects (New et al., 2007). This holds true even when statistically controlling for how interesting the target is perceived to be (New et al., 2007). Furthermore, this detection of animals is so rapid that it cannot be improved through training or familiarity with test images (Fabre-Thorpe et al., 2001). Humans are also faster at detecting the auditory calls of animals than artificial sound pulses, even when the sounds are matched for loudness (Suied et al., 2010). This is not simply explained by familiarity with the animal sounds, because detection speeds were just as rapid when white noise was acoustically modified using the low frequency soundwaves ("temporal envelopes") of the animal calls as templates. Subjects easily recognized these as artificial, non-animal sounds, suggesting that faster detection was facilitated by the sounds' acoustical properties, not their familiarity. Together, these studies suggest the brain is adapted to readily process stimuli that provided crucial fitness-related information to our evolutionary ancestors. This may be analogous to facial recognition, which is a highly heritable ability (Wilmer et al., 2010) that relies on dedicated brain areas (Liu et al., 2010).

Whether views of natural vistas are similarly processed more rapidly or efficiently than those of built environments has not been tested directly. However, consistent with nature scenery being less attentionally demanding, Berto et al. (2008) and Valtchanov and Ellard (2015) found that scenes of natural environments caused fewer eye fixations and saccades compared to when subjects viewed scenes of built environments, suggesting their eyes focused less on specific details. Furthermore, based on fMRI data, viewing photographs of built environments resulted in greater activation of brain regions involved with early stages of visual processing (inferior and middle occipital gyri [Kim et al., 2010a] and the lateral occipital area [Biederman and Vessel, 2006]) compared to photographs of natural settings. In contrast, brain regions involved in memory and reflection (the anterior cingulate gyrus and the precuneus) became more activated by nature images (Kim et al., 2010a), findings these authors suggest is evidence that nature scenery requires less concentration to interpret. In addition, the parahippocampal and rhinal cortices, both involved in memory and visual association, also became more activated when subjects viewed preferred nature scenes compared to anthropogenic images (Biederman and Vessel, 2006). These brain regions have a high density of μ -opioid receptors, which these authors hypothesize underlies "perceptual pleasure" experienced when viewing preferred scenes, particularly expansive views. Together, these studies support that nature scenery is processed with greater ease; however, they should be replicated with more carefully chosen images, since there was no attempt to control for the relative complexity, novelty or interest of the two image groups.

Lastly, again consistent with processing ease, research repeatedly demonstrates that natural environments enhance cognitive performance by facilitating recovery from mental fatigue (e.g. Berman et al., 2008; Kaplan, 1995). Various types of nature exposure have thus been found to improve performance in cognitively demanding tasks (i.e. tasks involving memory, directed attention and problem solving). The types of beneficial nature exposure include: photographs of natural vs. urban scenery (Berman et al., 2008; Berto, 2005); window views of natural vs. built scenery (Taylor et al., 2002; Tennessen and Cimprich, 1995); and exercise in natural vs. built environments (Berman et al., 2012; Berman et al., 2008; Bratman et al., 2015; Hartig et al., 1991). Furthermore, peoples' preferences for images of natural environments

are increased when they are mentally fatigued (Hartig and Staats, 2006; Staats et al., 2003). Again, rigorous fMRI research could help clarify the neurobiological bases for natural scenery's well documented restorative effects.

Joye and van den Berg (2011) argue that it is the coherent structure of natural environments that is effective here, contributing to so-called "processing fluency": a subjective experience of processing ease that is associated with positive affect (Duke et al., 2014; Reber et al., 1998; Winkielman and Cacioppo, 2001). Relevant factors experimentally found to improve both processing fluency and positive affect (inferred from zygomatic muscle activity) include congruent priming (Winkielman and Cacioppo, 2001) and stimulus repetition (Harmon-Jones and Allen, 2001). This positive affect occurs before the stimulus is even comprehended, suggesting that it is caused by the "dynamics of information processing" and not by the meaning of the content (Winkielman et al., 2003). This has even led to the proposal that aesthetic pleasure can be a direct function of processing dynamics (Reber et al., 2004). Positive stimulus evaluations (liking) are also increased by many other factors that increase processing fluency. These include contrast clarity, "prototypicality" (i.e. sharing similarities with familiar stimuli) and coherent patterns such as symmetry (reviewed by Winkielman et al., 2003; Winkielman and Huber, 2009).

One particular way in which natural views may be coherent is their tendency to contain many repeating patterns. More formally, the ease with which natural environments are processed is argued to reflect their "fractal" geometric structure (Joye, 2007; Joye and van den Berg, 2011; Purcell et al., 2001). Fractals are self-similar, meaning their structural properties repeat at smaller and smaller scales (Gisiger, 2001; Madelbrot, 1967). For example, when zooming in on a tree, branches appear as scaled down versions of the whole tree, and this is repeated as the branches taper out to their finest structures (Taylor et al., 2005). Although they are somewhat redundant and predictable, fractals are not monotonous: their patterns do not repeat exactly and are not distributed homogeneously, but tend to form clusters. Fractals are thought to result from dynamic processes that are intrinsic to nature (Bak et al., 1987; Gisiger, 2001). Aside from tree structures, they exist in many other natural phenomena including mountain ranges, coast line contours, clouds (Mandelbrot, 1967), or the size and distribution of gaps in rainforest canopies (Solé and Manrubia, 1995). Self-similar fractal structures also exist in time as well as space, and these properties have been identified in natural sounds (including running water), occurring as loudness modulation patterns and the relationship between the amplitudes and frequencies of component waves (Attias and Schreiner, 1997; Geffen et al., 2011). Such structural regularities in visual and auditory scenes of nature can be quantified. For example, when natural visual images are analysed for pixel intensity, luminance contrasts show predictable patterns across diverse images (Field, 1987). Visual and auditory neuroscience research suggests that sensory systems have evolved to exploit this statistical redundancy in the natural environment in order to maximize neural coding efficiency (reviewed by Atick, 1992; Reinagel and Laughlin, 2000; Simoncelli and Olshausen, 2001). Sensory systems are thus suggested to be finely-tuned to patterns in natural scenes, optimizing the allocation of neural resources and using processes comparable to digital data compression to eliminate self-similarity-generated redundancy from the neural code (Olshausen and Field, 2000). This proposal is supported by computational modelling (Lewicki, 2002; Olshausen and Field, 1996) and neuron recordings from live animals (Laughlin, 1981; Vinje and Gallant, 2002; Vinje and Gallant, 2000).

Overall, natural stimuli are thus suggested to have beneficial effects on health and well-being because of the ease with which human sensory organs and higher processing systems handle them. Because of this, they can reduce negative affective states resulting from overly intense activation of sense organs; help recovery from mental fatigue; and create positive affective states via processing fluency.

Table 2

Potential mechanisms by which preferred natural stimuli exert beneficial effects on humans, focusing on those likely to be relevant to other species.

Potential mechanism	Examples
Presence of specific beneficial components	Sunlight; plant volatiles; negative ions; beneficial bacteria
Meeting preferences	Views of water/vegetation are preferred as well as beneficial (see Table 1); this may be because ancestrally, these stimuli signified safety and plenty
Processing ease (potentially reducing sensory organ discomfort and cognitive fatigue)	Few/no aversive sensory properties (e.g. no overwhelming sounds, noxious chemicals, or visual flicker) Presence of wavelengths and intensities that sensory organs are well-designed to process Presence of repeated self-similar patterns (e.g. fractals) that are easy to process Presence of ancestrally familiar stimuli (e.g. animal sounds/shapes) that our brains have evolved to process efficiently

5.5. Summary

Diverse qualities of natural stimuli may account for their documented health and well-being benefits, which we have reviewed based on four potential explanations. First, specific natural products, including airborne molecules and beneficial bacteria' can have therapeutic or mood-improving qualities. Second, specific natural stimuli or landscapes may be positive primary reinforcers because evolutionarily, they signalled safety and resources. Third, the way that information is organized in real and depicted natural environments has properties that are preferred, possibly fulfilling innate desires to understand and explore, as well as indicating beneficial opportunities to interact with the environment. Fourth, sensory systems are argued to be specially adapted for processing natural stimuli, which is thought to directly promote relaxation and positive affect. The research findings presented in this section suggest differing, complementary levels of explanation rather than mutually exclusive alternatives. Furthermore many (those we summarise in Table 2) seem relevant to non-human animals housed in anthropogenic environments: the focus of the next section.

6. Potential benefits of natural stimuli for animal well-being

One obvious, albeit indirect, way in which certain natural stimuli could benefit laboratory or farm animals is by enhancing the workplace happiness of their human caretakers. After all, workers who are stressed, or keen to remove themselves from aversive environments, cannot be always expected to provide gentle, assiduous animal husbandry (cf. e.g. Hemsworth et al., 2009). However, our main focus is the *direct* influence that artificial environments could have on animal well-being. So far we have seen that humans' attraction to certain natural stimuli, and the benefits that these stimuli can have, do not appear to be culturally determined; and that they may stem from evolved preferences for cues signalling the availability of important resources (food, drinking water, safety) and/or evolved abilities to process such stimuli with ease. Together this makes it plausible that these human data may be extrapolated to other species. It is already well appreciated that unnaturally loud sounds (e.g. machinery), strong scents (e.g. cleaning products and concentrated manure gasses), and some attributes of artificial lighting, are all potential sources of stress or health problems for animals in farm, laboratory and other captive environments (e.g. Bakker et al., 2015; Hamilton et al., 1998; Kight and Swaddle, 2011; Morgan and Tromborg, 2007). But do certain types of natural stimuli actually *enhance* animal well-being? If they have effects analogous to those seen in humans, then they should be sought out by animals; reduce negative affective states like fear or anxiety; promote physiological recovery from acute stressors; and even reduce morbidity and mortality.

To reiterate, we are not naively suggesting that "naturalness" is always good. Perceived threats like snakes are natural, but they cause primates stress and fear (Van Le et al., 2013), and the same holds for predator cues (Dielenberg and McGregor, 2001; Morgan and Tromborg, 2007). The birdsong that humans find positive (e.g. in the auditory

research reviewed above) would typically be perceived as rivalrous challenge by conspecifics (Searcy and Beecher, 2009; Vehrencamp, 2001). Furthermore, animals kept outdoors can experience welfare problems that are less likely in indoor systems, like severe heat or cold stress (e.g. Arnott et al., 2016; Rochlitz, 2005; Van laer et al., 2014). That certain natural stimuli can promote animal welfare is thus not an assumption, but a hypothesis to be tested on a case by case basis. Next we therefore review what evidence there is for this idea.

6.1. Do animals seek out certain types of natural stimuli?

There is intuition among many experts that natural materials make especially good enrichments (e.g. Bracke et al., 2007), but few preference studies have addressed this question, let alone with the careful controls used in human research. In terms of preferences for being in natural environments, barn-housed dairy cattle given free access to pasture typically choose to spend most of their time outdoors (especially overnight), even though all their homeostatic needs could be met by staying in the barn (e.g. Charlton et al., 2011; Falk et al., 2012; Legrand et al., 2009). Furthermore, if required to push a heavily weighted door for access, cows reveal a high level of motivation: they will work as hard to reach pasture as they will to eat fresh food when hungry (working especially hard for overnight access; Von Keyserlingk et al., 2017). And they will continue to spend time outdoors even in very cold winter conditions (Shepley et al., 2016). Similar data come from other species, although these have been less well studied. Laying hens show a clear preference for outdoor runs over cages, independent of the type of environment they were reared in (Dawkins, 1977). Furthermore, in laboratory species, common marmosets in an Australian facility chose to spend more than two-thirds of their day in a small outdoor cage overlooking a small garden and parking lot. They did so even though this cage comprised only 20% of their space, and despite their indoor housing including a large enriched area (Pines et al., 2007). Another study on this species found that they still went outside daily, even during the cool north European winter (Bakker et al., 2015). Finally, although this does not appear to have been studied empirically, spending time outdoors seems reinforcing for cats and dogs (Jongman, 2007; Prescott et al., 2004). However, in all these cases, the space and complexity offered by the outdoor environments, and/or their thermal properties, may have been as or more important to the animals than any exposure to sun, wind, plants or natural vistas.

Turning to views *per se*, indoor-housed animals may choose to utilise windows to see outdoors (e.g. cats: Herron and Buffington, 2010; Jongman, 2007; Rochlitz, 2005; horses: Ninomiya et al., 2008; and laboratory primates: Prescott, 2006). Anecdotally, the famous African grey parrot 'Alex' would even say "Wanna go tree" in order to be carried to a window with a view (Morell, 2008). However, there is little empirical research on this topic, and nothing on the importance of the degree of 'naturalness' of the view. Research animals (primates and starlings) will also choose to view still images and videos, including ones depicting landscapes, water and animals. Movement, complexity, novelty, clarity, colour and views of conspecifics all emerge as preferred

visual properties (e.g. Blatter and Schultz, 2006; Funahashi, 2016; Kano and Tomonaga, 2009; Perret et al., 2015; Platt and Novak, 1997; Watanabe et al., 2016), but, again, whether the naturalness of the content adds value has not yet been explored.

Likewise, there has been little research into whether animals show preferences for specific natural stimuli. In one innovative experiment, laboratory rats were provided with climbing structures, shelters and manipulable objects that were either 'natural' (wood/pebbles) or 'artificial' (plastic/metal/twine). Although not given direct choices between these, rats provided with natural items did spend more time using them than did the rats with artificial equivalents (Lambert et al., 2016). However, whether this holds across other exemplars, such that 'naturalness' could really be said to be the preferred characteristic, is unknown. Capuchins, hens and pigs also prefer naturalistic flooring substrates like soil, peat, wood chips and chopped straw over hard surfaces (Dawkins, 1981; de Jong et al., 2006; Ludes-Fraulob and Anderson, 1999; Studnitz et al., 2007), but again it is uncertain whether 'naturalness' is truly the important attribute. As for naturalistic lighting, some birds housed indoors show preferences for full-spectrum lighting containing an ultraviolet component (perhaps because such lighting can aid in foraging and/or mate choice for species able to see UV; e.g. Jones et al., 2001; Maddocks et al., 2002; Moinard and Sherwin, 1999; Ross et al., 2013; but cf. Greenwood et al., 2002, and note that brightness is a confound in some of these studies). Furthermore, when outdoors, many birds are attracted to patches of sunlight in which they then show distinctive 'sun-bathing' postures (Kennedy, 1969; Naish, 2013; Stobbelaar and Hendriks, 2011), but this too has not been studied formally.

6.2. Can exposing animals to natural stimuli influence measures of stress, well-being or health?

Several studies suggest that living in or having access to the outdoors may confer welfare benefits to farmed, laboratory and companion animals (e.g. decreased mortality rates in cattle: Arnott et al., 2016; Dechow et al., 2011; decreased stereotypic behaviour and self-harm in rhesus monkeys: Fontenot et al., 2006; Gottlieb et al., 2013; O'Neill et al., 1991; Rommeck et al., 2009; and reduced rates of obesity, behavioural problems and some diseases in cats: Buffington, 2002; Rochlitz, 2005). However in every single case this treatment was confounded with other factors such as increased space or different management styles. Turning to vistas and visual stimuli, in zoos, polar bears in enclosures with outward views are less prone to stereotypic behaviour (Shepherdson et al., 2013) while clouded leopards with elevated vantage points have lower cortisol (Wielebnowski et al., 2002), but the content of the animals' views was not assessed in either study. More obviously relevant is a recent experiment in which wild-caught and hand-reared laboratory starlings were exposed to videos of natural landscapes (Coulon et al., 2014). However, effects were not clear-cut. Stereotypic behaviour declined in most of the wild-caught subjects, but not consistently across the whole group; indeed in hand-reared birds they increased, apparently because increased somersaulting – a movement thought to develop from escape attempts – was elicited by the videos.

Several studies have exposed laboratory, farm or zoo animals to specific tactile or auditory natural stimuli to assess effects on stress or health. For example, the naturally- versus artificially-enriched rats described in Section 6.1 were tested with challenging stimuli to assess their stress-resilience. The rats housed with wooden objects and pebbles appeared less anxious than those with artificial enrichments (Bardi et al., 2016; Lambert et al., 2016). Being exposed to grass also benefits rhesus monkeys: when outdoor-caged animals were housed in enclosures floored with either gravel or lawn, those with grass developed less alopecia, seemingly because it attracted sustained foraging, so distracting the animals from excessive grooming (Beisner and Isbell, 2008). Furthermore, pigs and primates given plant-based flooring

substrates in which to root and forage (e.g. woodchips or wood wool) show respectively less tail-biting and aggression (Studnitz et al., 2007), and more play (Ludes-Fraulob and Anderson, 1999). Note these are not panaceas however: when used in rodent cages, wood-based beddings can cause respiratory problems (Burn et al., 2006; Whiteside et al., 2010). Some researchers have also played rainforest noises to zoo-housed gorillas, but with mixed results: in one study, abnormal regurgitation and reingestion was reduced (Robbins and Margulis, 2014), but no such benefits were seen in other studies (e.g. Brooker, 2016), and indeed in two, the forest sounds apparently made animals agitated (reviewed Wells, 2009).

Using laboratory rodents, the effects of olfactory stimuli derived from plant volatiles (especially 'green odours') have been more extensively studied, with much of this very well-controlled research coming from Japan. With few exceptions, a consistent finding is that these odours reduce stress-reactivity (reviewed by Spiers et al., 2015). For example, in rats, green odours reduce the effects of restraint stress on corticosterone, ACTH, adrenal weight, core body temperature, maternal care and amygdala Fos expression (Fujita et al., 2010; Ito et al., 2009; Nakashima et al., 2004; Spiers et al., 2014), as well as the transient hyperthermia caused by being moved to a new cage (Akutsu et al., 2002, 2003). Green odours also reduce the emergence of learned helplessness in repeatedly stressed mice and rats (Nakatomi et al., 2008; Watanabe et al., 2011). Rose oil mitigated rats' corticosterone responses to restraint stress too (Fukada et al., 2012). Lavender oil, in contrast, was ineffective at reducing rats' hyperthermia responses to new cages (Akutsu et al., 2002); although in other species it has seemed beneficial, calming excitable dogs, reducing the symptoms of travel-sick pigs (reviewed by Wells, 2009) and decreasing heart rate in acutely-stressed horses (Ferguson et al., 2013).

Finally, several researchers have investigated two other properties of certain outdoor environments: the presence of sunlight (or of ultraviolet in artificial light, to mimic sunlight's spectral range), and increased levels of airborne negative ions. Sunlight or full spectrum lighting enhances Vitamin D production in a wide range of species (e.g. Arnott et al., 2016; Burild et al., 2016; Ferguson et al., 2002; Lewis and Gous, 2009; Woodhouse and Rick, 2016), although in mammals and birds this is not necessary if diets are properly fortified. Turning to negative air ionization, this improves indoor air quality, reducing dust, ammonia and airborne disease transmission in poultry barns (Gast et al., 1999; Ritz et al., 2006), and reducing influenza virus infectivity and airborne transmission in lab housed guinea pigs (Hagbom et al., 2015). A study in mice even suggests that water-generated negative ions act directly on the immune system: increasing natural killer cell activity and reducing growth of carcinogen-induced tumours (Yamada et al., 2006).

6.3. Summary

The hypotheses that animals prefer and benefit from exposure to natural environments (e.g. those containing plants and bodies of water) have not yet received much empirical investigation. In particular, research that teases out the effects of confounds (space, complexity, interest, etc.) is still lacking. Furthermore, a few studies even suggest that forced exposure to some natural stimuli can have counterproductive effects (e.g. rainforest sounds for gorillas and landscape videos for starlings may be frustrating or alarming), although if confirmed, this is perhaps rectifiable by offering such stimuli in ways that the animals themselves can control (cf. Cooper and Mason, 2001). Despite this, overall many circumstantial pieces of evidence, along with more specifically focussed findings in laboratory rodents (especially Bardi et al., 2016 and Lambert et al., 2016's enrichment research, and the impressive corpus of work on green odour), are at least *consistent* with animals choosing to experience certain natural elements and/or benefiting from such exposure. Such evidence makes this a potentially fruitful area for future research.

7. Conclusions and future research directions

As reviewed, a substantial body of evidence shows that humans prefer a range of natural stimuli and that these can beneficially influence affective states, physiological stress and health. Importantly, it is unlikely that culture or other learned factors are necessary to elicit these benefits, suggesting that human findings are relevant to other animals, such that providing preferred, species-relevant natural stimuli, via views, odours, sounds and enrichments, could represent effective new ways to improve animal welfare. However, this idea has so far received little direct empirical investigation. Experimental research on this topic is admittedly challenging, especially when the aim is to specifically attribute effects to properties that are inherently natural. Nevertheless, we believe that it is feasible, especially if modelled on the best-controlled human studies. Furthermore, for several reasons we believe such a research avenue could be very fruitful in terms of basic insights and understanding. First, the many animals currently raised in environments devoid of natural stimuli could provide convenient subjects for testing hypotheses related to the innateness of the effects discussed here. Furthermore, captive animals have diverse sensory biologies (e.g. some have far better olfactory abilities than our own, while others are sensitive to ultrasound or ultraviolet), and they also come from diverse evolutionary niches (across which the stimuli indicating safety and resources vary widely). This diversity, if combined with the use of ‘phylogenetic comparative methods’ (e.g. Mason, 2010), could allow the empirical testing of evolutionary hypotheses, including those related to ‘evolutionary signals’, ‘perceptual fit’ and ‘prospect-refuge’. Third, experiments could use animals to investigate the causal links between preference, changes in affective state, stress resilience, and health. Lastly, animal-based enrichment or stimulus-exposure studies could help uncover the neurobiological bases of natural stimuli preferences, and identify the neurobiological effects of long-term exposure, in order to determine if effects support some of the neurobiological hypotheses summarised in this review.

Such fundamental questions aside, research programs investigating the welfare benefits of certain natural stimuli could also deliver novel and practical strategies for improving managed animals’ resilience and well-being. Preventing captive animals from performing highly motivated behaviour patterns from their natural repertoires is already well-known to compromise welfare (e.g. Dawkins, 1990; Hughes and Duncan, 1988; Mason and Burn, 2011). Our proposal is that alongside these “behavioural needs”, animals may, just like the humans reviewed here, have “sensory needs”: preferences for certain natural stimuli that also benefit them (with effects that do not necessarily depend on direct behavioural interaction). Cheap and effective ways to improve health, stress-resilience and welfare could potentially emerge from studies into the effects of natural stimuli. These include adding specific natural elements *into* animals’ enclosures (e.g. wood items, other plant materials including peat and compost, and enrichments made of other natural materials); investigating the effects of the sensory environments *surrounding* animals’ enclosures (e.g. views, sounds, incoming ions and odours, and light quality, especially if also controllable); and from novel research into whether certain specific natural stimuli (e.g. green odours) could reduce the acute stress responses elicited by invasive or frightening procedures (e.g. handling, medical procedures and transportation).

In conclusion, natural stimuli have shaped animals’ evolution for millions of years, yet currently, billions of animals worldwide are kept in almost completely anthropogenic environments. In addition to generating novel fundamental insights, a research program into the welfare benefits of natural stimuli could thus yield new practical solutions to contemporary animal welfare problems.

Acknowledgements

We are grateful to Dr. Nathan Perkins who helped us review the literature on environment perception and landscape architecture. We

also thank Dr. Renée Bergeron, Dr. María Díez León and two anonymous referees for their very useful feedback on the manuscript. This work was financially supported by the Natural Sciences and Engineering Research Council of Canada, which had no further role in the manuscript preparation.

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