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Human well-being responses to species' traits

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People rely on well-functioning ecosystems to provide critical services that underpin human health and well-being. Consequently, biodiversity loss has profound negative implications for humanity. Human–biodiversity interactions can deliver individual-level well-being gains, equating to substantial healthcare cost savings when scaled up across populations. However, critical questions remain about which species and/or traits (for example, colours, sounds and smells) elicit well-being responses. The traits that influence well-being can be considered 'effect' traits. Using techniques from community ecology, we have analysed a database of species' effect traits articulated by people to identify those that generate different types of well-being (physical, emotional, cognitive, social, spiritual and 'global' well-being, the latter being akin to 'whole-person health'). Effect traits have a predominately positive impact on well-being, influenced by the identity and taxonomic kingdom of each species. Different sets of effect traits deliver different types of well-being. However, traits cannot be considered independently of species because multiple traits can be supported by a single species. Indeed, we have found that numerous effect traits from across the ecological community can elicit multiple types of well-being, illustrating the complexity of biodiversity experiences. Our empirical approach can help to implement interdisciplinary thinking for biodiversity conservation and nature-based public health interventions designed to support human well-being.

Multiple anthropogenic drivers are causing biodiversity loss worldwide[1]. Such biodiversity declines have profound consequences for ecosystem functioning and, consequently, the goods and services that underpin human health and well-being[2,3]. For instance, it is now widely accepted that interacting with nature (for example, in urban parks, forests and coastal areas) leads to stress relief, enhanced mood, improved cognitive ability and social cohesion, amongst an array of other benefits[4,5]. Such evidence is accumulating from across the world, including from low-, middle- and high-income countries[6]. When these individual-level gains in health and well-being are scaled up to entire populations, they can equate to substantial cost savings for the public health sector. This is pertinent in locations where the prevalence of mental ill health is particularly high (for example, in Europe[7]) and given that human well-being is a predictor of both life expectancy and mortality[8,9].

Despite abundant research demonstrating that interactions with nature benefit human well-being, we still lack conclusive empirical evidence regarding the role of biodiversity specifically. Biodiversity is the living component of nature, incorporating "the diversity within species, between species and of ecosystems"[10]. Many existing studies

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use proxy measures of nature, such as remotely sensed 'green space'[11,12], revealing correlative associations with well-being across large-scale cross-sections of the human population. However, these macroscale approaches treat green spaces as homogeneous entities, overlooking the fact that people's relationships with biodiversity are both contextually and culturally specific[13]. The context relates to the physical and ecological place-based characteristics of a green space, which can be highly variable within and between ecosystems of the same type[14]. How a person responds to a green space will also be influenced by personal, societal and cultural associations, as well as previous experiences[13,15]. Understanding how people experience biodiversity is therefore key to successfully managing biodiversity to facilitate human well-being, incorporating it into sustainable land-use planning initiatives[16], nature-based solutions and social ('green') prescribing interventions[17].

Following the 'biopsychosocial–spiritual' model of health, which is adapted from medicine[18,19], human well-being is thought to comprise five separate domains: physical (the body and how someone feels physically), emotional (positive and negative mood), cognitive (state of mind), social (perceived connections with others) and spiritual (relationships with one's self or something greater than one's self). People's multisensory experiences of biodiversity may elicit both positive and negative responses in one or more of these well-being domains[20]. For instance, hearing the song of a male European robin (*Erithacus rubecula*) might prompt a positive emotional response (for example, joy), while the stinging hairs of a common nettle (*Urtica dioica*) may provoke a negative physical response (for example, physical discomfort). Each species, however, may support multiple traits, potentially with independent impacts (for example, robins sing and have plumage that is red in colour, each trait potentially stimulating a different type of well-being). Studies of biodiversity–well-being relationships must thus consider the ecological community that makes up a green space in its entirety, moving beyond just single traits (for example, flower colour[21]) and/or taxonomic groups (for example, birds[22–24]) and towards combinations of traits across multiple taxa simultaneously. The subsequent compound effects on multiple types of human well-being would then better reflect the real-world experience of interacting with biodiversity in a particular place.

Ecologists have traditionally examined how the biotic and abiotic environment influences species traits ('response traits')[25]. Some, but not all, of these traits also function to supply ecosystem services ('effect traits') (for example, proboscis length of insect pollinators and pollination efficiency)[26]. Species' traits that directly elicit human well-being responses could therefore be considered effect traits. The functional effect of a species on an ecosystem is thought to be proportional to its contribution to total biomass across the ecological community (that is, the effect traits of dominant species drive ecosystem function, the so-called mass ratio hypothesis[27]). Species may also occupy functionally distinct niches, using available resources in a complementary way (niche complementarity hypothesis[28]). Across species, there may also be overlap in effect traits that deliver multiple functions (multifunctionality), within and across different ecosystem service classes[29–32]. Ecological communities can subsequently be examined for redundancy (where species delivering the same functions as others become functionally redundant/exchangeable) and complementarity (optimal combinations of species that deliver the maximum services). Such an approach is useful when designing cost-efficient conservation actions and allocating resources to support the delivery of specific ecosystem services. While well established for regulating and provisioning ecosystem services, only a handful of studies have examined effect traits for cultural ecosystem services (the identities, capabilities and experiences that people actively create and express through interactions with ecosystems[33]), and those studies have either been restricted to a single taxon (birds) or have not measured well-being as an outcome[22,24].

Table 1 | Definitions of the self-reported human well-being domains

Well-being type	Definition
Physical	The physical body and how one feels physically
Emotional	Positive and negative emotion and mood
Cognitive	A person's state of mind
Social	How one perceives their connection with others
Spiritual	Relationship with one's self or something greater than one's self
Global	Unspecified sense of overall health/well-being (or lack thereof)

The five domains (physical, emotional, cognitive, social and spiritual) originate from the biopsychosocial–spiritual model of health[18]. We also identified 'global' well-being, akin to the concept of whole-person health from integrative medicine[35,36], which recognizes a sense of overall health/well-being (or lack thereof).

Here we demonstrate a novel analytical approach through which the linkage between species' effect traits in an ecological community and human well-being can be examined at a granular level. We asked two questions. (1) Which species' effect traits relate to each type of human well-being? (2) To what extent are species, and the effect traits they exhibit, redundant or complementary in the delivery of human well-being? We held a series of participatory workshops, one per season (winter, spring, summer and autumn), with a diverse cross-section of the public ($n = 194$). During each workshop, participants were taken to the same two British forests. We then documented how the species' traits identified by participants elicited self-reported positive and negative responses across the five well-being domains (physical, emotional, cognitive, social and spiritual; Table 1). We also identified 'global' well-being[34], recognizing that these multiple domains are interdependent in contributing to how one feels overall (akin to the idea of 'whole-person health', an overall sense of health/wellness[35,36]). We used the words of participants when documenting incidences of species' effect traits eliciting well-being. For example, one row of data is formed when a participant describes a negative physical response (allergy) to the behaviour (blossoming) of an elder (*Sambucus nigra*): "some fluffy stuff on it which set off my hay fever in the spring so I don't like those".

Our study centred on forest ecosystems, which declined in areal extent by 31.6% globally between 1990 and 2015 due to deforestation, fragmentation and other pressures[37]. Today, forests cover approximately one-third of global terrestrial surface area and support ecosystem services valued at ~9% of global gross domestic product[38]. Including cultural service benefits within such assessments remains a challenge, particularly given the diverse ways in which people relate to nature, yet this is crucial for creating conservation policies that are inclusive of the people they seek to benefit[3].

Results

Identifying species' effect traits

Participants articulated 102 unique effect traits (Table 2) across 403 species (taxonomic kingdoms: animals, fungi and plants) eliciting a well-being response ($n = 1,815$ unique effect trait–well-being combinations). Of these effect traits, colours (for example, pink, gold and silver), and behaviours (for example, hopping, decaying and elusive) had the greatest variety (29.4% each), followed by sounds (for example, creaking, chirping and screaming; 19.6%), with a smaller number of textures (for example, smooth, spongy and prickly; 14.7%) and smells (for example, damp, pine and sweet; 6.9%) mentioned. However, sounds most frequently stimulated well-being responses (40.4%), above behaviours (26.5%), colours (23.7%), textures (7.3%) and smells (2.1%; Fig. 1a). This reveals the relative importance of forest sounds for well-being over the other effect trait types. It is possible that sounds could be more conspicuous than other effect traits for species that are difficult to

Table 2 | Definitions of trait types and example effect traits

Trait type	Definition	Example of effect traits
Texture	About the qualities of the surface of something	Prickly, feathers, stinging
Colour	Any mention of colour	Red, blue, colourful
Behaviour	Anything that moves or changes	Decaying, pupating, moving
Smell	What something smells or does not smell like	Earthy, garlic, clean
Sound	Focus on natural sounds	Buzzing, birdsong, rustling

Definitions of trait types coded in the transcripts from four workshops that took place in winter, spring, summer and autumn of 2019 after participants (n=194) visited two forests geographically located in a central region of Great Britain. Example effect traits mentioned by participants are provided for each trait type.

encounter directly in forest vegetation. Additionally, it highlights the role of species' behaviours, which have received very little research attention in relation to well-being.

Redundancy and complementarity

Over 85% of effect trait–well-being combinations were positive, spanning physical, emotional, cognitive, social, spiritual and global well-being, but particularly spiritual well-being (Fig. 1a). Indeed, there were comparatively few negative effect trait–well-being combinations (Fig. 1a). Moreover, a high level of redundancy (plateauing lines) was reached after relatively few species for negative types of well-being (Fig. 1b). This suggests that a small number of species were sufficient to deliver negative well-being, with little additional impact arising from greater numbers of species in the ecological community. This plateau also implies that all the species and effect traits that elicit negative well-being were documented through our methodology. In contrast, the inclines for positive emotional and spiritual well-being imply there are still more effect traits and species to be captured. Some 'keystone' tree species supported a disproportionate number of unique effect traits, particularly silver birch (*Betula pendula*), horse chestnut (*Aesculus hippocastanum*) and English oak (*Quercus robur*; Extended Data Fig. 1). However, as each additional species brings with it additional effect traits, this suggests that maintaining diversity in forest ecosystems is beneficial for human well-being (Fig. 1b).

By visualizing the data, we found that some effect traits were similar in the frequency with which they elicited different types of well-being, resulting in clusters (for example, sounds in Fig. 1c). These patterns were explained mostly by the species exhibiting the effect trait (23.1%), the type of trait (colour, texture, sound, smell and behaviour; 16.2%) and taxonomic kingdom (animal, plant and fungi) of the species (10.0%), thereby triangulating our understanding of how people relate to forest biodiversity[13] (Extended Data Fig. 2). Furthermore, the sets of effect traits that linked to each type of well-being were significantly different (P = 0.001 for each pair; Fig. 1c). We quantified this dissimilarity using Sørensen's index (>0.5, pink shades in Fig. 2). These differences support the niche complementarity hypothesis[28], whereby specific effect traits deliver largely unique types of well-being. Such detail could be used to improve the design of nature-based public health interventions, by managing ecosystems for the species that exhibit particular effect traits (for example, alterations to the biodiversity in a particular place where people interact with nature, such as planting regimes in public parks designed to enhance cognitive restoration[39]).

However, each species may comprise multiple effect traits. When we calculated the Sørensen's index between the identities of species for each type of well-being, there were high levels of similarity (<0.5, green shades in Fig. 2). Some species therefore influence multiple types of well-being. For example, the tawny owl (*Strix aluco*), whose "calling" and "communicating" sounds alongside its "using trees" behaviour elicited three different positive types of well-being (physical, cognitive and spiritual). In some cases, species caused both positive and negative types of well-being: the colours ("black", "pink" and "red") of bramble plants (*Rubus fruticosus*) linked to multiple positive well-being types (physical, emotional and social), while its "prickly" texture generated negative well-being (emotional). In one instance, the "tweeting" effect trait of passerine bird species was an indicator of both positive and negative spiritual well-being (Supplementary Table 1). By contrast, Sørensen's index for both the effect traits and species that elicited negative physical well-being were largely dissimilar from all other types of well-being (0.71–1 and 0.84–0.99, respectively). One inference that could be drawn from this finding is that such species and their associated effect traits could be removed from forests to improve human well-being. However, this would have potentially profound adverse consequences for biodiversity conservation and the functioning of ecosystems, given that these species and their effect traits could be influencing the delivery of multiple ecosystem services across different classes (for example, provisioning and regulating) that were not examined in this study.

Discussion

Our approach, working across an ecological community, exposed granular levels of detail on how species functionally deliver well-being benefits. Effect trait–well-being incidences depend on the identity of the species and taxon supporting each effect trait, and it is therefore not possible to disaggregate effect traits from the species that host them when it comes to determining whether, and how, human well-being is delivered. Moreover, our findings show that numerous effect traits from across the ecological community can elicit a multitude of well-being types, as well as global well-being, illustrating the true complexity of the biodiversity experience. It is possible that multiple effect traits may also interact, resulting in additive or multiplicative impacts on human well-being (for example, the cumulative effect of smells alongside sounds from one or more species), which warrants future investigation. Such intricacies could be further detailed by measuring the strength of an effect trait (for example, light to dark red, thus accounting for phenotypic variation within species), as well as by measuring levels of human well-being. This identification of thresholds could better inform public health recommendations (for example, ref. 40) and align our study with those examining how differing levels of, and interactions between, multiple effect traits modulate levels of regulating and provisioning ecosystem service benefits[26,31].

Our participatory methodology identified the multitude of ways in which people experience biodiversity and positive/negative well-being in particular places. However, our study participants also related to species' effect traits encountered in the forests through their past experiences with the same/similar species' effect traits outside of the workshops in other locations (for example, memories of childhood, at home or on holiday). This emphasizes the need for researchers to incorporate such pluralism into ecosystem services assessments[3,41], as well as the need for inclusive land-use planning initiatives, nature-based solutions and green prescriptions.

Our approach is a step change in how biodiversity has been considered in biodiversity–health/well-being research so far, moving away from a focus on a limited set of taxa (for example, birds), biodiversity metrics (for example, species richness) or specific types of trait (for example, colour or sound)[21,42]. The multiplicity of species' effect traits, and their influence on well-being, captured by sampling participants from a diverse range of socio-demographic/economic backgrounds, emphasized the variation in how people experience forest biodiversity. The rich variation in species' effect traits was also augmented by holding our participatory workshops across the course of a year, ensuring that any influence of seasonal variation in the conspicuousness of species and, therefore, effect traits was covered by the study design (for example, the colour blue of bluebells *Hyacinthoides non-scripta* and the winter plumage of birds). These approaches are likely to reveal a

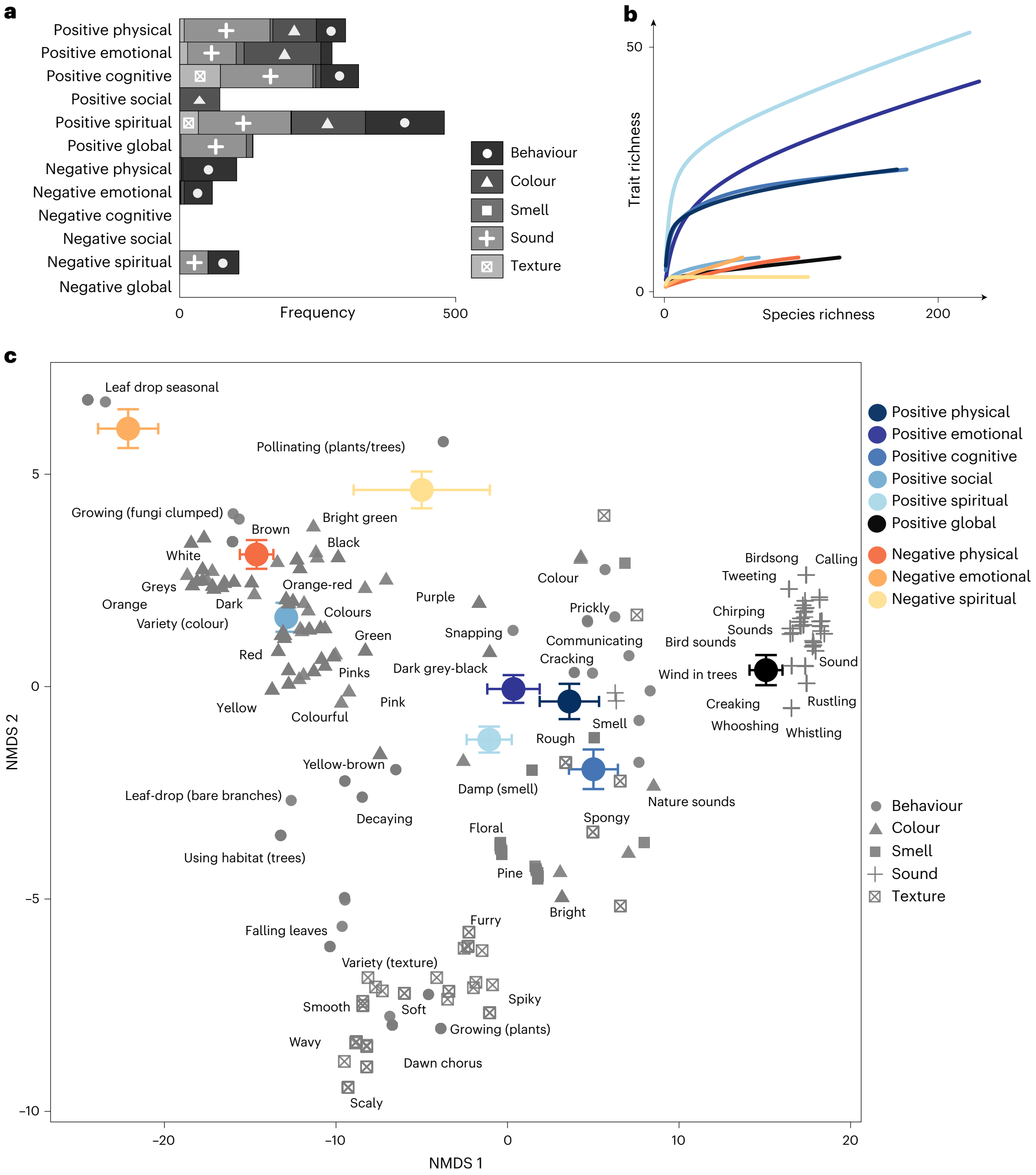
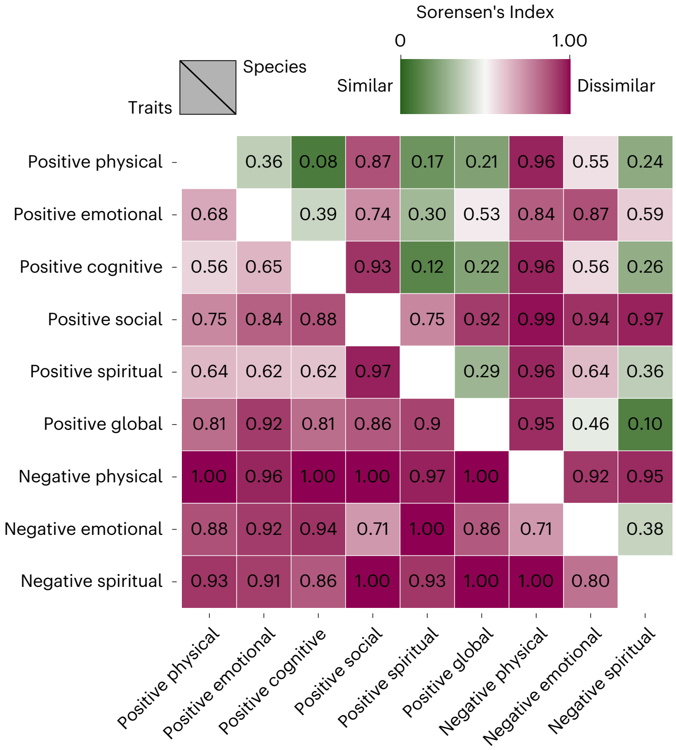


Fig. 1 | The contribution of species' effect traits to different types of human well-being. Effect traits eliciting a well-being response, with $n = 1{,}815$ unique effect trait–well-being combinations. **a**, The number of unique effect trait–well-being combinations broken down by effect trait type and well-being type. **b**, The shape of the species–effect trait relationship for each type of well-being. For the line colour code, see **c**. **c**, Ordination based on non-metric multidimensional scaling (NMDS) of a Bray–Curtis dissimilarity matrix. The positions of points (effect trait–well-being combinations, shaped by trait type) represent dissimilarity in the number of incidences that effect traits elicited different types of well-being. The labelled effect traits are indicators of each well-being type (Supplementary Table 1). Large circles represent mean centroids for each well-being type, with horizontal and vertical error bars showing 95% confidence intervals. A low level of stress (<0.05) indicated excellent fit. Note, no incidences meant it was not possible to create centroids for negative cognitive, social or global well-being.

further array of effect traits that influence people's well-being in different ways when applied to other ecosystems (for example, a prevalence of negative physical well-being from allergenic tree or grass pollen in urban ecosystems, particularly in summer). This opens avenues for further research into how biodiversity–well-being linkages could be affected by climatic variability influencing ecological phenology and processes[29,43].

Forest restoration is one of twelve targets for maintaining Life on Land (Sustainable Development Goal 15 (ref. 44)) and has become a policy focus globally. A surfeit of regional, national and international initiatives have been devised and implemented to retain, restore and create forests, pledging to plant billions of trees worldwide[45,46]. Yet these interventions could have low success rates and/or fail to meet anticipated outcomes[44]. While these initiatives often seek to



	Positive physical	Positive emotional	Positive cognitive	Positive social	Positive spiritual	Positive global	Negative physical	Negative emotional	Negative spiritual
Positive physical		0.36	0.08	0.87	0.17	0.21	0.96	0.55	0.24
Positive emotional	0.68		0.39	0.74	0.30	0.53	0.84	0.87	0.59
Positive cognitive	0.56	0.65		0.93	0.12	0.22	0.96	0.56	0.26
Positive social	0.75	0.84	0.88		0.75	0.92	0.99	0.94	0.97
Positive spiritual	0.64	0.62	0.62	0.97		0.29	0.96	0.64	0.36
Positive global	0.81	0.92	0.81	0.86	0.9		0.95	0.46	0.10
Negative physical	1.00	0.96	1.00	1.00	0.97	1.00		0.92	0.95
Negative emotional	0.88	0.92	0.94	0.71	1.00	0.86	0.71		0.38
Negative spiritual	0.93	0.91	0.86	1.00	0.93	1.00	1.00	0.80	

Fig. 2 | The (dis)similarity of effect traits and species contributing to different types of human well-being. Sørensen's similarity index for sets of effect traits (lower left triangle) and species (upper right triangle) contributing to different types of well-being. Similarity on a scale from 0 (similar, green) to 1 (dissimilar, pink).

provide the so-called 'triple wins' for climate change, biodiversity and human well-being[47,48], many neglect to consider their social and cultural impacts[46,49,50]. Indeed, without support from those who live in and interact with the landscape, it will be more difficult for restoration and conservation initiatives to succeed. Our findings highlight that biodiversity will not be beneficial for everyone in the same way, which needs to be accounted for in forest restoration policies if they are to deliver both equitable and socially just outcomes. These potential trade-offs between conservation and societal goals can be better informed by granular levels of detail about which species' effect traits benefit people, as well as the other ecosystem functions and services that they support.

We found that compared with other forest taxa (for example, insects and birds), participants described trees as having a disproportionately large number of unique effect traits that stimulated well-being responses. This is likely attributable to the year-round visibility of trees, with effect trait diversity enhanced by seasonal changes and longevity[13]. This has important implications for the conservation of forests and trees, particularly those that are old growth. Moreover, tree species are likely to comprise the dominant biomass of such ecosystems, therefore supporting the mass ratio hypothesis[27]. Species-rich boreal and temperate forests also support high levels of provisioning ecosystem services, with no single species able to deliver them all[51]. When combined with our study, this demonstrates the multifunctionality of forests and trees, critical to reinforcing national and global policy initiatives to conserve, enhance and restore forests and trees for both people and nature.

Managing the biodiversity within ecosystems to select for species' effect traits that benefit human well-being has potentially important implications for conservation. For instance, removing the species and effect traits that elicit negative physical well-being may have knock-on negative implications for the ecosystem (for example, disrupting symbiotic relationships or trophic interactions). Furthermore, species with substantial aesthetic value or prominent cultural meaning may be less ecologically or evolutionarily distinct, non-native or not of conservation interest[52]. In practice, trade-offs may have to be made. If we are to manage ecosystems to promote well-being, extreme care needs to be taken to ensure that there are no unintended adverse consequences for biodiversity conservation and the functioning of ecosystems, given that species' effect traits can be operating across multiple other classes of ecosystem service.

One potential limitation of our study is that many mental processes are unconscious, meaning that people may sometimes mistakenly attribute cause and effect, relying on existing beliefs or expectations that may be biased or contain errors of judgement[53,54]. Such phenomena could mean that there were inaccuracies in the way our participants articulated species' effect traits eliciting well-being responses. Nonetheless, a growing body of literature has demonstrated links between biodiversity and improved objective measures of health and well-being (for example, visiting a sensory garden led to reductions in physiological stress, measured via salivary cortisol[55], and a higher density of urban street trees was linked to reduced antidepressant prescription rates[56]).

Here we have detailed an empirical approach revealing how the biodiversity in a particular place underpins human well-being, which can help to inform how ecological communities could be managed to promote different well-being outcomes. Our approach can be operationalized to create better-tailored public health interventions or architectural/landscape designs (for example, maximizing the likelihood of interactions with certain species), while reducing health inequalities and promoting socially inclusive natural environments[41]. From a conservation standpoint, it further illustrates the functional consequences of biodiversity loss for human well-being, while raising debate about the consequences of manipulating ecological communities for human benefit. However, our approach can be harnessed to optimize conservation solutions, such as ecological restoration[57], biodiversity net gain[58] and systematic conservation planning[59], for both social and ecological outcomes. We therefore provide a novel grounding for advancing our understanding of, and integration between, the fields of environmental psychology, functional ecology and their wider cultural dimensions (for example, as cultural ecosystem services). Such interdisciplinary thinking is pivotal if we are to effectively move towards a more sustainable and equitable society in the face of global environmental change.

Methods

Study system

This study centred on forests, the focus of several global policy initiatives to conserve and enhance forest carbon in the face of climate change, including the Reducing Emissions from Deforestation and Forest Degradation[60], the Sustainable Development Goals[61], and the United Nations Decade on Ecosystem Restoration[38]. Forest restoration and creation (tree-planting) schemes are rapidly gaining traction, but overlook the social and political implications these policies have on people[47], despite requiring public support to succeed[46]. In the United Kingdom, there are 3.2 Mha of forests and woodlands, split between broadleaf (49%) and coniferous (51%) habitat[62]. They are generally publicly accessible, and are amongst the most frequently visited outdoor spaces in the country[63]. We took participants from across the country to two forests, geographically located in a central region of Great Britain, to ensure encounters with a diversity of traits: Sherwood Forest (an ancient woodland) and Clumber Park (a managed mixed-deciduous and coniferous plantation forest). These forests were selected as their objective physical and biological characteristics varied and they were not 'local' to any of the participants. This was a purposeful decision to maximize the variety of place-based characteristics (species and traits) within and across the two ecosystems, and to minimize the potential influence that previous experience of the forests might have had on the participants' well-being responses to the objective qualities of the place.

Workshop participants

Participants ($n = 194$) were recruited via a social research agency between February and October 2019. Individuals were selected across gender (male = 92, female = 102), ethnicity (white = 146, other = 48), age (18–29 years = 60, 30–59 years = 68, 60+ years = 66), region of residence (Scotland = 11, Wales = 10, England = 173), social grade (AB = 56, C1 = 58, C2 = 42, DE = 38), and urban and rural living (urban = 153, rural = 41). The social grades are defined as follows: AB, higher and intermediate managerial, administrative, and professional occupations; C1, supervisory, clerical and junior managerial, administrative, and professional occupations), C2 (skilled manual occupations) and DE (semi-skilled and unskilled manual occupations and unemployed). All participants had to have been living in Great Britain for at least 5 years, irrespective of their nationality. Our approach meant we captured the diversity of the British public, including sectors of society that are often underrepresented in research (for example, elderly, ethnic minorities and lower income earners)[64]. To encourage workshop attendance and promote inclusivity, participants were incentivized by travel reimbursement and financial remuneration to cover their time with us.

Participants were split over four weekend-long workshops ($n = 46$–50 per workshop) across the year (winter = February, spring = May, summer = July, autumn = October), with activities designed to stimulate discussion about forest biodiversity (but not well-being specifically). Participants took part in a 1-hour scavenger hunt in situ, in which they were asked to record what they noticed in terms of, for example, smells, colours, textures and sounds. We asked participants to focus on biotic attributes (for example, biodiversity) rather than anthropogenic (for example, pathways). While participants undertook these activities alone, they were then divided into small groups to discuss their impressions of forest biodiversity together. We encouraged participants to expand on why they noticed certain traits. The conversation topics raised by participants expanded upon their experiences outside of the workshops (for example, memories of childhood, at home or on holiday), thus widening the diversity of species referenced. On the second day, participants undertook multiple image-based Q methodology activities[13,15] designed to stimulate further discussion about species traits and preferences ex situ, followed by discussions about different trait types.

Qualitative analyses

All audio-recorded activities were transcribed and imported into NVivo (Version 12, QSR International). We then coded where participants had discussed specific trait types (for example, texture, colour, behaviour, smells or sounds; Table 2). We also coded where participants self-reported positive or negative sentiments, as well as discussed benefits/disbenefits to their well-being following the biopsychosocial–spiritual model of health (Table 1). This model accounts for five different domains of human well-being (physical, emotional, cognitive, social and spiritual), which can be both positive and negative (Supplementary Table 2)[18,19,34]. References to 'global' well-being were also reported (sense of overall health/well-being, or lack thereof)[35,65] and classed as an additional code[34].

Identifying species' effect traits

For each of the trait types, we extracted all relevant references from NVivo. For each reference, we then identified the species to which the participant was referring (for example, the specific species shown in the Q-methodology pictures[13] or a species named by the participant). We then identified the particular effect trait (for example, "slimy") mentioned in relation to each species, using the participants' own words. We disregarded references to abiotic factors such as running water, rain or wind, but retained statements when abiotic factors were related to living things (for example, "wind in the trees"). Traits were aggregated when the terms had alternative endings (for example, the sound "screaming" contained "scream", "screams" and "screaming") or were synonymous (for example, the texture "gnarly" contained "gnarly", "gnarled" and "twisted") to create a standardized final list of traits. This final list was agreed upon by all co-authors. Using the well-being codes, we were able to show whether traits had been linked to a particular valence (positive or negative) and type of well-being (physical, emotional, cognitive, social, spiritual or global). We then cross-referenced when traits and species were spoken about in relation to valence and well-being codes, creating a data matrix of binary responses (1 or 0 for each well-being type) for each mention of a species' effect trait. If two participants made different comments about the same species' effect trait eliciting the same type of well-being, this would aggregate to two incidences. For analyses, the matrix was formatted to display species–well-being combinations as rows, with the corresponding effect traits as column headers, populated by values that represented the cumulative number of incidences across participants.

Species mentioned by participants that did not occur in British forests were removed from the data (for example, locusts *Schistocerca gregaria* and monkey puzzle tree *Araucaria araucana*). When participants only described particular phenological elements (for example, acorns), we made inferences about the associated species name (for example, acorns were listed as English oak *Quercus robur*). When participants made general references to a collective group of organisms, we consulted reputable sources (Supplementary Table 4) to derive a list of species with that trait (for example, participants noticed the trait "spots" on "birds", from which we generated a list of 13 species of British forest birds that had spots). When deriving this extended list, we excluded species that were rare occurrences, accidental records, passage or scarce visitors. We did not generate lists of species for traits that were too generic across an entire taxonomic group (for example, trees that were "green").

Statistical analyses

All statistics were conducted in R (version 4.3.0, https://www.r-project.org/). To quantify the variety of effect traits for each trait type, we summed the number of unique effect traits for each trait type, then calculated proportions using the total number of unique effect traits. To investigate the shape of the species–trait relationship, we plotted accumulation curves of trait and species richness for each type of well-being (function 'accumcomp' in package BiodiversityR[66]). To visually explore the association between traits and different types of well-being, we used NMDS (function 'metaMDS' in package vegan[67]). An NMDS is an iterative ordination analysis that uses rank orders and can be applied to a variety of data types[68]. In our case, it enabled a visual interpretation of the relative number of incidences of effect traits linked to different types of well-being in two-dimensional space. We did not transform the data before analysis (recommended for non-ecological data)[69], but calculated a matrix of Bray–Curtis dissimilarity coefficients to input into the NMDS. A measure of 'stress' was used to determine how well the points in the NMDS are represented across two-dimensional space, determining model fit (the stress in our model was <0.05, indicating very good representation[70]). We also plotted the species (and taxonomic kingdom) that supported these effect traits, in relation to each well-being type, and examined the approximate directional relationship between the well-being types and the species' effect traits in k-dimensional space by overlaying the well-being types as vector arrows (function 'envfit' in the package vegan[67] with 999 permutations; Extended Data Fig. 2).

We used permutational multivariate analysis (ADONIS, function 'adonis' in package BiodiversityR[66]) to investigate predictors (species, taxonomic kingdom and trait type) of the visualized trait–well-being patterns (Fig. 1c). Next, we tested whether differences in the visualized patterns of effect traits between each type of well-being were significantly different, conducting a pairwise permutational multivariate analysis (PERMANOVA, function 'pairwise.perm.manova' in the package RVAideMemoire[71] with 999 permutations). To quantify the extent of any overlap, we calculated Sørensen's similarity index[72] (function 'vegdist' in package vegan[67]) for the effect traits, as well as species that elicited each pair of well-being types. This index produces continuous values that range from 1 (highly dissimilar) to 0 (very similar).

We identified which effect traits contributed to the dissimilarities identified. We carried out an indicator analysis (function 'indicators' in the package Indicspecies[73]) to determine which species' effect traits were significantly associated with each type of well-being. This function produces an indicator value that can range between 0 and 1, where 1 represents a circumstance where all mentions of the effect trait are in relation to this well-being type only, and mentions of the effect trait are in every elicitation of this well-being type.

Ethics

Workshop participants provided written informed consent before data collection. Ethics approval was provided by the School of Anthropology and Conservation Research Ethics Committee, University of Kent (ref: 009-ST-19).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data are available from the following repository: https://doi.org/10.22024/UniKent/01.01.479.

References

1. *Global Assessment Report on Biodiversity and Ecosystem Services* (IPBES, 2019); https://doi.org/10.5281/ZENODO.3831673
2. Horton, R. & Lo, S. Planetary health: a new science for exceptional action. *Lancet* **386**, 1921–1922 (2015).
3. Díaz, S. et al. Assessing nature's contributions to people. *Science* **359**, 270–272 (2018).
4. Lovell, R., Depledge, M. & Maxwell, S. *Health and the Natural Environment: A Review of Evidence, Policy, Practice and Opportunities for the Future* 1–161 (Defra, 2018); http://randd.defra.gov.uk/
5. *Urban Green Spaces and Health: A Review of Evidence* (World Health Organization, 2016); https://apps.who.int/iris/handle/10665/345751
6. Nawrath, M., Guenat, S., Elsey, H. & Dallimer, M. Exploring uncharted territory: do urban greenspaces support mental health in low- and middle-income countries? *Environ. Res.* **194**, 81–96 (2021).
7. Wittchen, H. U. & Jacobi, F. Size and burden of mental disorders in Europe—a critical review and appraisal of 27 studies. *Eur. Neuropsychopharmacol.* **15**, 357–376 (2005).
8. Diener, E. & Chan, M. Y. Happy people live longer: subjective well-being contributes to health and longevity. *Appl. Psychol. Health Well-Being* **3**, 1–43 (2011).
9. Steptoe, A., Deaton, A. & Stone, A. A. Subjective wellbeing, health, and ageing. *Lancet* **385**, 640–648 (2015).
10. *Kunming-Montreal Global Biodiversity Framework* (CBD, 2022), https://www.cbd.int/doc/c/e6d3/cd1d/daf663719a03902a9b116c34/cop-15-l-25-en.pdf
11. Helbich, M., de Beurs, D., Kwan, M. P., O'Connor, R. C. & Groenewegen, P. P. Natural environments and suicide mortality in the Netherlands: a cross-sectional, ecological study. *Lancet Planet. Health* **2**, e134–e139 (2018).
12. Maes, M. J. A. et al. Benefit of woodland and other natural environments for adolescents' cognition and mental health. *Nat. Sustain.* **4**, 851–858 (2021).
13. Austen, G. E. et al. Exploring shared public perspectives on biodiversity attributes. *People Nat.* **3**, 901–913 (2021).
14. Wheeler, B. W. et al. Beyond greenspace: an ecological study of population general health and indicators of natural environment type and quality. *Int. J. Health Geogr.* **14**, 17 (2015).
15. Austen, G. E. et al. The diversity of people's relationships with biodiversity should inform forest restoration and creation. *Conserv. Lett.* https://doi.org/10.1111/conl.12930 (2022).
16. Giles-Corti, B. et al. City planning and population health: a global challenge. *Lancet* **388**, 2912–2924 (2016).
17. Garside, R. et al. *Therapeutic Nature: Nature-Based Social Prescribing for Diagnosed Mental Health Conditions in the UK* (Defra, 2020); http://randd.defra.gov.uk/
18. Linton, M.-J., Dieppe, P. & Medina-Lara, A. Review of 99 self-report measures for assessing well-being in adults: exploring dimensions of well-being and developments over time. *BMJ Open* **6**, e010641 (2016).
19. Engel, G. The need for a new medical model. *Science* **196**, 129–136 (1977).
20. Irvine, K. N. et al. BIO-WELL: the development and validation of a human wellbeing scale that measures responses to biodiversity. *J. Environ. Psychol.* **85**, 101921 (2023).
21. Hoyle, H. et al. Plant species or flower colour diversity? Identifying the drivers of public and invertebrate response to designed annual meadows. *Landsc. Urban Plan.* **180**, 103–113 (2018).
22. Echeverri, A. et al. Can avian functional traits predict cultural ecosystem services? *People Nat.* **2**, 138–151 (2020).
23. Leong, R. A. T. et al. Use of structural equation modeling to explore influences on perceptions of ecosystem services and disservices attributed to birds in Singapore. *Ecosyst. Serv.* **46**, 101211 (2020).
24. Zoeller, K. C., Gurney, G. G., Heydinger, J. & Cumming, G. S. Defining cultural functional groups based on perceived traits assigned to birds. *Ecosyst. Serv.* **44**, 101138 (2020).
25. Violle, C. et al. Let the concept of trait be functional! *Oikos* **116**, 882–892 (2007).
26. Lavorel, S. et al. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *J. Veg. Sci.* **24**, 942–948 (2013).
27. Grime, J. P. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86**, 902–910 (1998).
28. Tilman, D., Wedin, D. & Knops, J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720 (1996).
29. Duncan, C., Thompson, J. R. & Pettorelli, N. The quest for a mechanistic understanding of biodiversity–ecosystem services relationships. *Proc. R. Soc. B* **282**, 20151348 (2015).
30. Gross, N. et al. Functional trait diversity maximizes ecosystem multifunctionality. *Nat. Ecol. Evol.* **1**, 0132 (2017).
31. Felipe-Lucia, M. R. et al. Multiple forest attributes underpin the supply of multiple ecosystem services. *Nat. Commun.* **9**, 4839 (2018).
32. Soliveres, S. et al. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* **536**, 456–459 (2016).
33. Fish, R. D., Church, A. & Winter, M. Conceptualising cultural ecosystem services: a novel framework for research and critical engagement. *Ecosyst. Serv.* **21**, 208–217 (2016).
34. Irvine, K. N., Warber, S. L., Devine-Wright, P. & Gaston, K. J. Understanding urban green space as a health resource: a qualitative comparison of visit motivation and derived effects among park users in Sheffield, UK. *Int. J. Environ. Res.* **10**, 417–442 (2013).
35. Langevin, H. M. Making connections to improve health outcomes. *Glob. Adv. Health Med.* **11**, 2164957X221079792 (2022).
36. Thomas, H., Mitchell, G., Rich, J. & Best, M. Definition of whole person care in general practice in the English language literature: a systematic review. *BMJ Open* **8**, e023758 (2018).

37. *Global Forest Resources Assessment 2015: How Are the World's Forests Changing?* (FAO, 2016).
38. *The State of the World's Forests 2022. Forest Pathways for Green Recovery and Building Inclusive, Resilient and Sustainable Economies* (FAO, 2022); https://doi.org/10.4060/cb9360en
39. Shanahan, D. F. et al. Nature-based interventions for improving health and wellbeing: the purpose, the people and the outcomes. *Sports* **7**, 141 (2019).
40. White, M. P. et al. Spending at least 120 minutes a week in nature is associated with good health and wellbeing. *Sci. Rep.* **9**, 7730 (2019).
41. Neuteleers, S. & Hugé, J. Value pluralism in ecosystem services assessments: closing the gap between academia and conservation practitioners. *Ecosyst. Serv.* **49**, 2016–2017 (2021).
42. Methorst, J., Bonn, A., Marselle, M. R., Böhning-Gaese, K. & Rehdanz, K. Species richness is positively related to mental health—a study for Germany. *Landsc. Urban Plan*. **211**, 104084 (2021).
43. Isbell, F. et al. Linking the influence and dependence of people on biodiversity across scales. *Nature* **546**, 65–72 (2017).
44. Duguma, L. et al. *From Tree Planting to Tree Growing: Rethinking Ecosystem Restoration Through Trees* (World Agroforestry, 2020); https://doi.org/10.5716/WP20001.PDF
45. Endreny, T. A. Strategically growing the urban forest will improve our world. *Nat. Commun.* **9**, 1160 (2018).
46. Seddon, N. et al. Getting the message right on nature-based solutions to climate change. *Glob. Change Biol.* **27**, 1518–1546 (2021).
47. Pritchard, R. Politics, power and planting trees. *Nat. Sustain* **4**, 932 (2021).
48. Zhang, J., Fu, B., Stafford-Smith, M., Wang, S. & Zhao, W. Improve forest restoration initiatives to meet Sustainable Development Goal 15. *Nat. Ecol. Evol.* **5**, 10–13 (2021).
49. Coleman, E. A. et al. Limited effects of tree planting on forest canopy cover and rural livelihoods in Northern India. *Nat. Sustain.* **4**, 997–1004 (2021).
50. Erbaugh, J. T. et al. Global forest restoration and the importance of prioritizing local communities. *Nat. Ecol. Evol.* **4**, 1472–1476 (2020).
51. Gamfeldt, L. et al. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* **4**, 1340 (2013).
52. Langlois, J. et al. The aesthetic value of reef fishes is globally mismatched to their conservation priorities. *PLoS Biol.* **20**, e3001640 (2022).
53. Nisbett, R. E. & Valins, S. in *Attribution: Perceiving the Causes of Behavior* 63–78 (eds Jones, E. E. et al.) (Lawrence Erlbaum Associates, 1987).
54. Nisbett, R. E. & Wilson, T. D. Telling more than we can know: verbal reports on mental processes. *Psychol. Rev.* **84**, 231–259 (1977).
55. Souter-Brown, G., Hinckson, E. & Duncan, S. Effects of a sensory garden on workplace wellbeing: a randomised control trial. *Landsc. Urban Plan.* **207**, 103997 (2021).
56. Marselle, M. R. et al. Urban street tree biodiversity and antidepressant prescriptions. *Sci. Rep.* **10**, 22445 (2020).
57. Laughlin, D. C. Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecol. Lett.* **17**, 771–784 (2014).
58. Bull, J. W., Hardy, M. J., Moilanen, A. & Gordon, A. Categories of flexibility in biodiversity offsetting, and their implications for conservation. *Biol. Conserv.* **192**, 522–532 (2015).
59. Decker, E., Linke, S., Hermoso, V. & Geist, J. Incorporating ecological functions in conservation decision making. *Ecol. Evol.* **7**, 8273–8281 (2017).
60. Corbera, E. & Schroeder, H. Governing and implementing REDD+. *Environ. Sci. Policy* **14**, 89–99 (2011).
61. Griggs, D. Sustainable development goals for people and planet. *Nature* **495**, 305–307 (2013).
62. Reid, C. et al. *State of the UK's Woods and Trees 2021* (Woodland Trust, 2021).
63. *Monitor of Engagement with the Natural Environment: The National Survey on People and the Natural Environment. Headline Report 2019* (Natural England, 2019).
64. Fischer, L. K. et al. Recreational ecosystem services in European cities: sociocultural and geographical contexts matter for park use. *Ecosyst. Serv*. 455–467 (2018).
65. Thomas, H., Mitchell, G., Rich, J. & Best, M. Definition of whole person care in general practice in the English language literature: a systematic review. *BMJ Open* **8**, e023758 (2018).
66. Kindt, R. & Coe, R. Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies (World Agroforestry Centre, 2005).
67. Oksanen, J. et al. vegan, R package version 2.5-2 (2018); https://CRAN.R-project.org/package=vegan
68. Nguyen, L. H. & Holmes, S. Ten quick tips for effective dimensionality reduction. *PLoS Comput. Biol.* **15**, e1006907 (2019).
69. Warton, D. I., Wright, S. T. & Wang, Y. Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol. Evol.* **3**, 89–101 (2012).
70. Kenkel, N. C. & Orloci, L. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology* **67**, 919–928 (1986).
71. Hervé, M. RVAideMemoire: Testing and Plotting Procedures for Biostatistics, R package version 0.9-81-2 (2022); https://CRAN.R-project.org/package=RVAideMemoire
72. Sørensen, T. A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *K. Dan. Vidensk. Selsk. Skr.* **5**, 1–34 (1948).
73. De Cáceres, M. & Legendre, P. Associations between species and groups of sites: indices and statistical inference. *Ecology* **90**, 3566–3574 (2009).

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Author contributions

Z.G.D., M.D., K.N.I. and R.D.F. conceptualized the study and acquired the funding. J.C.F., Z.G.D., M.D. and K.N.I. developed the methodology. J.C.F., S.G.A. and P.M.K. curated and interpreted the data. J.C.F. was responsible for the software and undertook the visualization, formal analysis and writing of the original draft paper. Z.G.D. and M.D. were supervisors, while Z.G.D. and G.E.A. were responsible for project administration. All authors contributed to the investigation, as well as the reviewing and editing of the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41893-023-01151-3.

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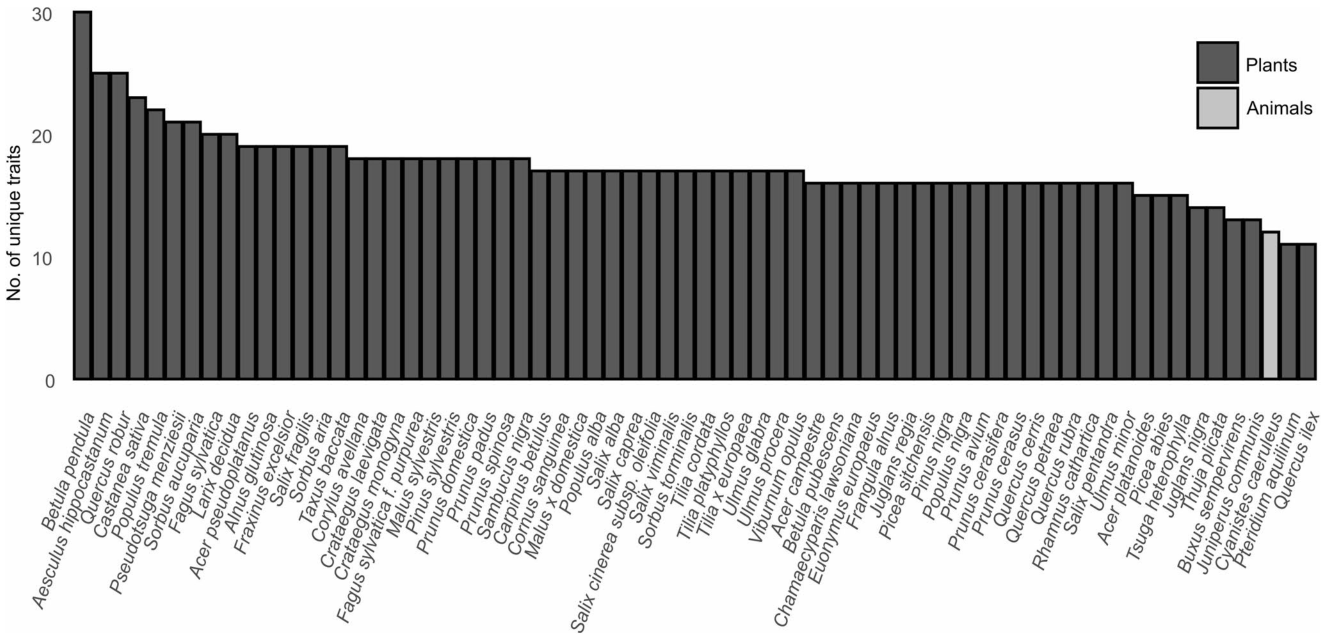
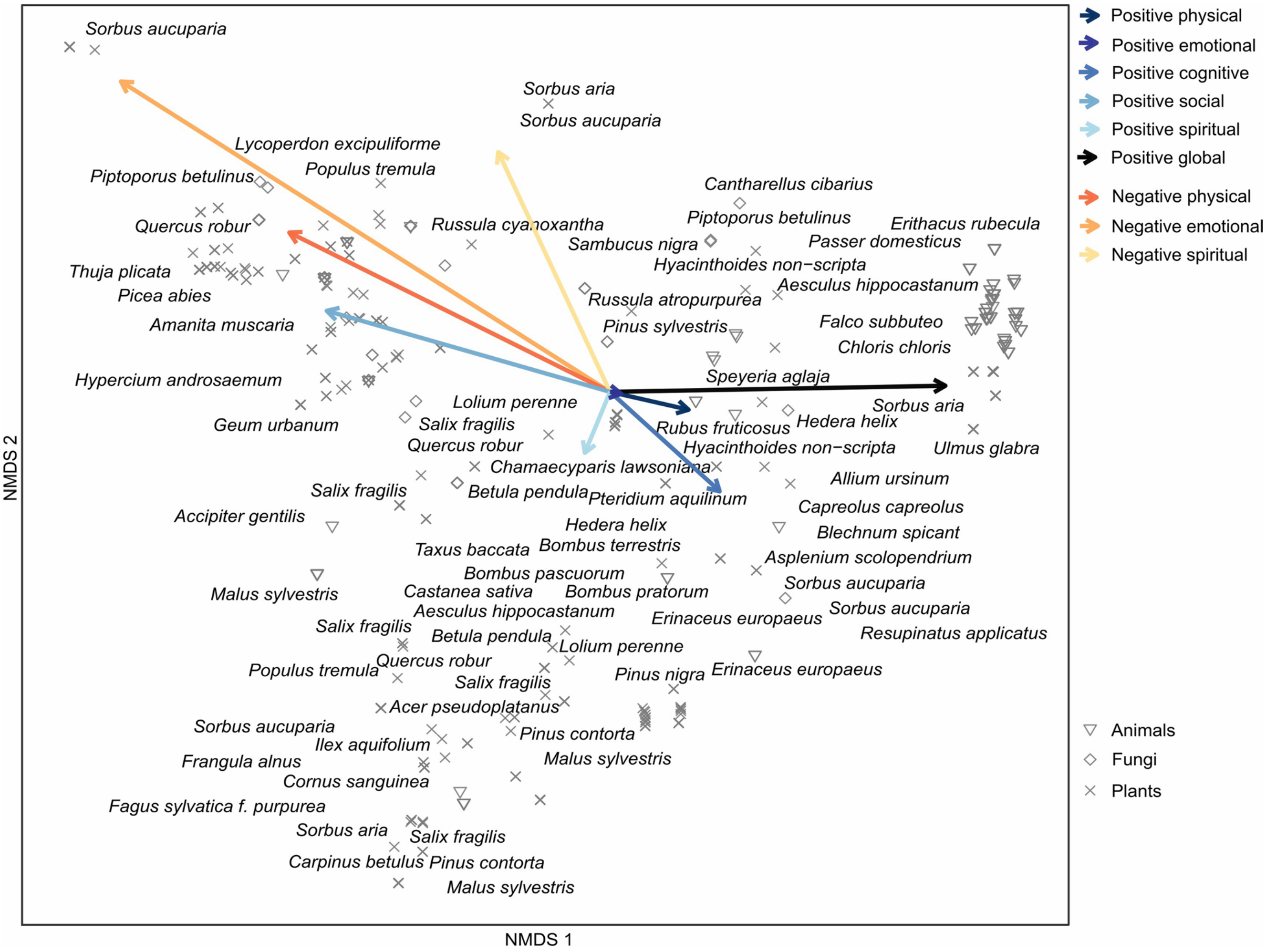


Extended Data Fig. 1 | The number of unique effect traits that elicit wellbeing mentioned by participants for each species, across all taxonomic groups. Species with the greatest number of unique effect traits, irrespective of taxonomic group, as derived from participant ($n = 194$) discussions during a series of workshops held across the four seasons in 2019.



Extended Data Fig. 2 | The contribution of species' effect traits to different types of human wellbeing. Species supporting effect traits that elicit a wellbeing response, with $n = 1815$ unique trait-wellbeing combinations. Ordination based on non-metric multidimensional scaling (NMDS) of a Bray-Curtis dissimilarity matrix. The position of points (trait-wellbeing combinations, shaped by taxonomic kingdom of species that supports each effect trait; animal = triangle, fungi = diamond, plant = cross) represent dissimilarity in the number of incidences that effect traits elicited different types of wellbeing. A low level of stress (< 0.05) indicted excellent fit. Wellbeing types are overlaid as vector arrows. NB: no incidences meant it was not possible to create vector arrows for negative cognitive, social or global wellbeing. Not all labels shown due to overlap. Full list of species' Latin and common names can be found in Supplementary Information Table 3.

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Software and code

Policy information about availability of computer code

Data collection	No software were used for data collection
Data analysis	Qualitative analyses were conducted in NVIVO version 12 (QSR International). Statistical analyses were conducted in R version 4.3.0 (https://www.r-project.org/), using the following packages: BiodiversityR (version 2.15-1); Vegan (version 2.6-4); RVAideMemoire (version 0.9-21-2); Indicspecies (version 1.7.12).

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The datasets generated during and/or analysed during the current study are available from the corresponding author upon reasonable request.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	Data were collected for gender (shaped by social and cultural circumstances), as determined by participants' self-reporting. Individuals were selected to ensure diversity of perspectives from the public across gender (male = 90, female = 103, prefer not to say = 1), but testing for differences between gender per se was not within the scope of this study. Participants provided written informed consent prior to data collection.
Population characteristics	Individuals were from diverse genders (male = 92, female = 102), ethnicities (white = 146, other = 48), ages (18-29 years = 60, 30-59 years = 68, 60+ years = 66), regions of residence (Scotland = 11, Wales = 10, England = 173), social grades (AB = 56, C1 = 58, C2 = 42, DE = 38), and urban-rural living (urban = 153, rural = 41). Social grade is defined as: AB (higher and intermediate managerial, administrative, professional occupations), C1 (supervisory, clerical, and junior managerial, administrative, and professional occupations), C2 (skilled manual occupations), and DE (semi-skilled and unskilled manual occupations, unemployed).
Recruitment	Participants (n = 194) were recruited via a social research agency between February and October 2019. Individuals were selected to ensure diversity of perspectives from the public. To encourage workshop attendance and inclusivity, participants were incentivised by travel reimbursement and financial renumeration. This may have biased the sample to participants who did not work weekends (thus our analyses may not accurately represent this sector of society), or those who wished to attend workshops that involved visiting woodlands (thus biasing our findings to those with an open mind). However, we still documented negative experiences, and incidences where participants did not enjoy visits to woodlands, thus negating such bias.
Ethics oversight	Ethics approval was provided by the School of Anthropology and Conservation Research Ethics Committee, University of Kent (Ref: 009-ST-19).

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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Behavioural & social sciences study design

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Study description	This is a mixed methods study. We firstly used a participatory research approach with a cross-section of the British public, collecting qualitative data. These transcripts were then coded, before being transformed into a quantitative matrix, analysed using ecological techniques.
Research sample	Perspectives of biodiversity are known to vary between different socioeconomic and demographic groups. Therefore, individuals

Research sample	were selected to ensure a diversity of perspectives from the British public, with some intentional oversampling on groups that are typically underrepresented (e.g. ethnic minorities, lower income earners, elderly).
Sampling strategy	The sampling procedure was stratified, based on simple quotas provided to the social research agency. No sample-size calculation was performed as the dataset was originally qualitative. The sample of participants for the workshops (n = 194) was based the resources available for hosting participants away, across a weekend. However, this sample is unusually large for a qualitative study, and therefore deemed sufficient to represent a diverse set of responses from across the British public.
Data collection	Participants took part in a 1-hour scavenger hunt in-situ (Sherwood Forest and Clumber Park), and given paper, pen, and a clipboard. Following these visits, participants were divided into focus groups to discuss their impressions of the forest, recorded using a Dictaphone device. On the second day participants undertook multiple image-based Q-methodology activities (see Austen et al. 2021) using paper and pens. Facilitators were present during the data collection, but were not blind to the study hypotheses.
Timing	Participants were split over four weekend-long workshops (n = 46-50 per workshop) across the year (winter = 02/19, Spring = 05/19, Summer = 07/19, Autumn = 10/19).
Data exclusions	No participants were excluded from the analyses.
Non-participation	Six participants were unable to attend the workshops due to personal circumstances or weather inhibiting the ability to travel.
Randomization	Participants were randomly allocated into focus groups.

Ecological, evolutionary & environmental sciences study design

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Sampling strategy	*Note the sampling procedure. Describe the statistical methods that were used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient.*
Data collection	*Describe the data collection procedure, including who recorded the data and how.*
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Field work, collection and transport

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Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Antibodies

Antibodies used	*Describe all antibodies used in the study; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Validation	*Describe the validation of each primary antibody for the species and application, noting any validation statements on the manufacturer's website, relevant citations, antibody profiles in online databases, or data provided in the manuscript.*

Eukaryotic cell lines

Policy information about cell lines and Sex and Gender in Research

Cell line source(s)	*State the source of each cell line used and the sex of all primary cell lines and cells derived from human participants or vertebrate models.*
Authentication	*Describe the authentication procedures for each cell line used OR declare that none of the cell lines used were authenticated.*
Mycoplasma contamination	*Confirm that all cell lines tested negative for mycoplasma contamination OR describe the results of the testing for mycoplasma contamination OR declare that the cell lines were not tested for mycoplasma contamination.*
Commonly misidentified lines (See ICLAC register)	*Name any commonly misidentified cell lines used in the study and provide a rationale for their use.*

Palaeontology and Archaeology

Specimen provenance	*Provide provenance information for specimens and describe permits that were obtained for the work (including the name of the issuing authority, the date of issue, and any identifying information). Permits should encompass collection and, where applicable, export.*
Specimen deposition	*Indicate where the specimens have been deposited to permit free access by other researchers.*
Dating methods	*If new dates are provided, describe how they were obtained (e.g. collection, storage, sample pretreatment and measurement), where they were obtained (i.e. lab name), the calibration program and the protocol for quality assurance OR state that no new dates are provided.*

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Ethics oversight	*Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	*For laboratory animals, report species, strain and age OR state that the study did not involve laboratory animals.*
Wild animals	*Provide details on animals observed in or captured in the field; report species and age where possible. Describe how animals were caught and transported and what happened to captive animals after the study (if killed, explain why and describe method; if released, say where and when) OR state that the study did not involve wild animals.*
Reporting on sex	*Indicate if findings apply to only one sex; describe whether sex was considered in study design, methods used for assigning sex. Provide data disaggregated for sex where this information has been collected in the source data as appropriate; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex-based analyses where performed, justify reasons for lack of sex-based analysis.*
Field-collected samples	*For laboratory work with field-collected samples, describe all relevant parameters such as housing, maintenance, temperature, photoperiod and end-of-experiment protocol OR state that the study did not involve samples collected from the field.*
Ethics oversight	*Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Clinical data

Policy information about clinical studies

All manuscripts should comply with the ICMJE guidelines for publication of clinical research and a completed CONSORT checklist must be included with all submissions.

Clinical trial registration	*Provide the trial registration number from ClinicalTrials.gov or an equivalent agency.*
Study protocol	*Note where the full trial protocol can be accessed OR if not available, explain why.*
Data collection	*Describe the settings and locales of data collection, noting the time periods of recruitment and data collection.*
Outcomes	*Describe how you pre-defined primary and secondary outcome measures and how you assessed these measures.*

Dual use research of concern

Policy information about dual use research of concern

Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes	
☒	☐	Public health
☒	☐	National security
☒	☐	Crops and/or livestock
☒	☐	Ecosystems
☒	☐	Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes	
☒	☐	Demonstrate how to render a vaccine ineffective
☒	☐	Confer resistance to therapeutically useful antibiotics or antiviral agents
☒	☐	Enhance the virulence of a pathogen or render a nonpathogen virulent
☒	☐	Increase transmissibility of a pathogen
☒	☐	Alter the host range of a pathogen
☒	☐	Enable evasion of diagnostic/detection modalities
☒	☐	Enable the weaponization of a biological agent or toxin
☒	☐	Any other potentially harmful combination of experiments and agents

ChIP-seq

Data deposition

☐ Confirm that both raw and final processed data have been deposited in a public database such as GEO.

☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links *May remain private before publication.*	*For "Initial submission" or "Revised version" documents, provide reviewer access links. For your "Final submission" document, provide a link to the deposited data.*
Files in database submission	*Provide a list of all files available in the database submission.*
Genome browser session (e.g. UCSC)	*Provide a link to an anonymized genome browser session for "Initial submission" and "Revised version" documents only, to enable peer review. Write "no longer applicable" for "Final submission" documents.*

Methodology

Replicates	*Describe the experimental replicates, specifying number, type and replicate agreement.*
Sequencing depth	*Describe the sequencing depth for each experiment, providing the total number of reads, uniquely mapped reads, length of reads and whether they were paired- or single-end.*
Antibodies	*Describe the antibodies used for the ChIP-seq experiments; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Peak calling parameters	*Specify the command line program and parameters used for read mapping and peak calling, including the ChIP, control and index files used.*
Data quality	*Describe the methods used to ensure data quality in full detail, including how many peaks are at FDR 5% and above 5-fold enrichment.*
Software	*Describe the software used to collect and analyze the ChIP-seq data. For custom code that has been deposited into a community repository, provide accession details.*

Flow Cytometry

Plots

Confirm that:

☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

☐ All plots are contour plots with outliers or pseudocolor plots.

☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	*Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.*
Instrument	*Identify the instrument used for data collection, specifying make and model number.*

Software	*Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.*
Cell population abundance	*Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.*
Gating strategy	*Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.*

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type	*Indicate task or resting state; event-related or block design.*
Design specifications	*Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.*
Behavioral performance measures	*State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).*

Acquisition

Imaging type(s)	*Specify: functional, structural, diffusion, perfusion.*
Field strength	*Specify in Tesla*
Sequence & imaging parameters	*Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.*
Area of acquisition	*State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.*

Diffusion MRI ☐ Used ☐ Not used

Preprocessing

Preprocessing software	*Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).*
Normalization	*If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.*
Normalization template	*Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.*
Noise and artifact removal	*Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).*
Volume censoring	*Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.*

Statistical modeling & inference

Model type and settings	*Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).*
Effect(s) tested	*Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.*

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Statistic type for inference (See Eklund et al. 2016)	*Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.*
Correction	*Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).*

Models & analysis

n/a	Involved in the study
☐	☐ Functional and/or effective connectivity
☐	☐ Graph analysis
☐	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity	*Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).*
Graph analysis	*Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).*
Multivariate modeling and predictive analysis	*Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.*