A global synthesis of trends in human experience of nature

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The popular perception that humans are undergoing a global extinction of "experience of nature" (EoN) is poorly supported by empirical evidence. Here, we provide – to the best of our knowledge – the first global systematic review of trends in EoN, identifying only 18 studies that measured temporal trends in EoN. Of those 18 studies, several reported negative trends over time for both direct EoN (for example, in-person visits to parklands) and vicarious EoN (specifically, the presence of nature in cultural products, such as movies or books), and all were biased toward North America, Western Europe, and Japan. As an initial proxy for understudied regions, we calculated past trends in three metrics of global EoN opportunities and show that, over the past decades, the locations where humans live have shifted away from the natural world and become more urban, while forest cover in cities has decreased. Overall, our results suggest that while EoN may be declining globally, existing evidence is insufficient to assess the magnitude and generality of this phenomenon.

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The ongoing destruction and degradation of natural systems, along with biodiversity loss, are largely attributable to human activities (Díaz *et al.* 2019). In order to reduce human impacts on global biodiversity, there is growing interest in identifying the factors that increase people's concern for environmental issues and promote pro-environmental behaviors (Bamberg and Möser 2007; Gifford and Nilsson 2014; Clayton and Myers 2015). Among these factors, "experience of nature" (EoN) is known to affect human values and attitudes by reinforcing individuals' psychological and emotional connection with nature (Clayton and Myers 2015). For instance, a high level of EoN in childhood strongly shapes people's knowledge of, values toward, and emotional attachment to nature (Wells and Lekies 2006; Chawla 2009); moreover, people with extensive EoN were more likely to adopt pro-environmental behaviors (Prévot *et al.* 2018a) and have a strong environmental identity (Prévot *et al.* 2018b).

In a nutshell:

- Human "experience of nature" (EoN) is thought to be declining worldwide, reflecting troubling signs of human disconnection from nature, but this claim is poorly supported
- A systematic literature search yielded only 18 studies, which provided evidence that nature presence in cultural products was declining, but examinations of direct EoN were rare
- Trends in EoN remain unstudied in more than half of the world's countries, and we contend that EoN may be in especially sharp decline in those regions
- There is an urgent need to strengthen assessments of global trends in EoN

However, EoN appears to be in decline globally, with humans becoming increasingly disconnected from nature, as part of a broader process or syndrome referred to as the "extinction of experience" (Pyle 2003; Miller 2005), which may have serious consequences in terms of humans' emotions, values, and attitudes toward nature (Soga and Gaston 2016). Although the extinction of experience is often assumed as genuine in the scholarly literature, evidence supporting the global decline of EoN is scarce (Gaston and Soga 2020) and to date has not been assessed systematically. The most recent review on the extinction of experience, that of Soga and Gaston (2016), provided a handful of examples of negative trends in EoN; however, that study was not intended to be exhaustive, as its primary objective was to address the causes and consequences of the process.

Conducting a systematic assessment of evidence in support of the extinction of experience is now crucial, not only to determine whether EoN is truly on the decline globally but also – and perhaps more importantly – to analyze this presumed phenomenon at finer scale. Indeed, trends in EoN might differ widely among countries due to variations in economic situations, traditional ways of life, or degrees of interaction with nature (Pyle 2003). To test whether the extinction of experience is indeed global or restricted to certain regions, researchers must therefore investigate the spatial heterogeneity of trends in EoN. In addition, EoN assumes a diversity of forms, some of which are direct (eg spending time in nature) while others are vicarious (eg watching a wildlife documentary); moreover, different types of "nature" are experienced, ranging from urban parks to genuinely wild and remote areas

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(Gaston and Soga 2020). Thus, while certain types of EoN may be in decline, others may be on the rise, and it is essential that this diversity be taken into account, as they may have different sensory and emotional implications that trigger a variety of responses among individuals.

Here, we provide what we believe to be the first systematic synthesis of recent trends in EoN in order to test whether the extinction of experience phenomenon is real by (1) reviewing empirical studies investigating trends in EoN and mapping their spatial distribution; (2) performing a meta-analysis of the strength of these trends, as well as their heterogeneity depending on the type of EoN studied; and (3) filling critical knowledge gaps across the world by mapping trends in three metrics of EoN opportunities, which are known to be key predictors of EoN (Soga and Gaston 2016).

Systematic review and meta-analysis of empirical studies

We conducted a systematic review to identify studies that provide evidence of temporal trends in EoN or the presence of nature in cultural products. In this paper, we define EoN as direct or vicarious interactions between humans and nature that may foster an individual's relationship with (Nisbet *et al.* 2009) and/or knowledge about (Bögeholz 2006) nature, and the subsequent development of pro-environmental attitudes (Barragan-Jason *et al.* 2022). This definition does not consider the level of an individual's engagement with nature, unlike definitions that require the individual to be, as Gaston and Soga (2020) stated, "engaged in the interaction on an emotional, physical, spiritual or intellectual level". We chose this definition because temporal studies that investigated trends in EoN (that is, those used to support the extinction of experience principle) have focused mostly on interactions and not on their effects on individuals, which are more difficult to measure.

Following PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-analyses) recommendations (O'Dea *et al.* 2021), we searched Web of Science and PubMed for papers assessing trends in EoN published from 1900 to 2021, with search terms corresponding to the various keywords that appeared in previously published reviews and opinions: namely, extinction of experience; green space AND decline; green space AND increase; outdoor AND decline; outdoor AND increase; recreation* activit*; urban nature AND decrease, urban nature AND increase; recreation* AND decline; and recreation* AND increase (WebPanel 1). In addition to the 957 papers obtained by the above-mentioned protocol, we also screened 500 separate papers that cited a key reference, that of Miller (2005). Of these 1457 identified papers, we selected only those reporting temporal trends in EoN or nature presence in cultural products; a total of 18 studies met our inclusion criteria (Figure 1). To quantify trend strength, we conducted meta-analyses of effect sizes when data were available. To do so, we performed a Spearman correlation between EoN and time of publication of seven papers, and mean differences of five papers when only two observations were available (WebPanel 1; Figure 2).

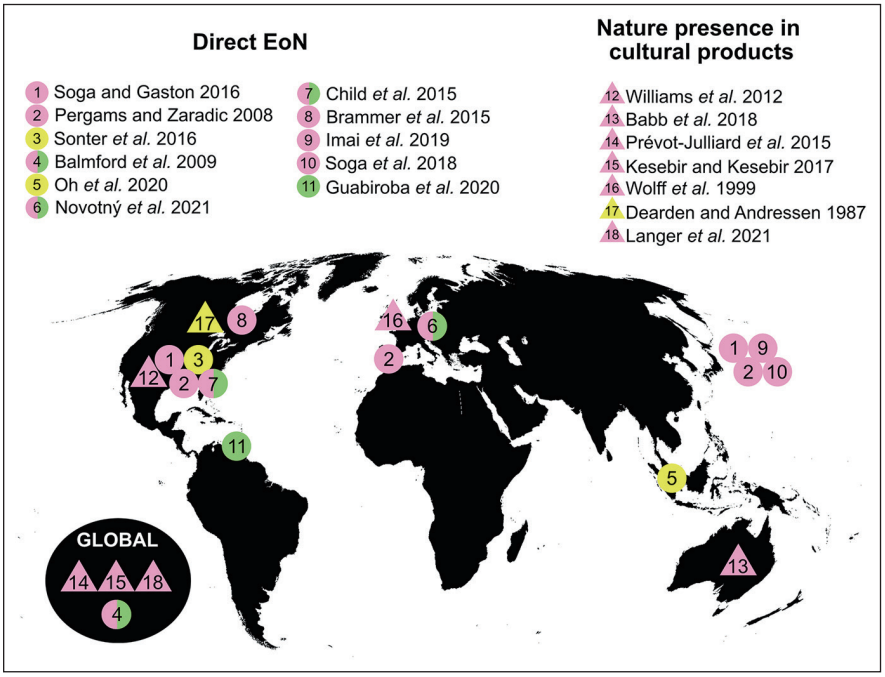

Figure 1. Distribution of published evidence (n = 18 studies) of experience of nature (EoN) trends detected in our systematic review. Positive trends (that is, increases in EoN) are shown in green, negative trends in pink, and neutral trends in yellow. Circles indicate direct EoN, whereas triangles indicate one type of vicarious EoN (nature presence in cultural products).

Direct EoN through outdoor activities

Of the eleven identified studies measuring trends in direct EoN, several measured (and reported mostly negative) trends in visits to parklands. For instance, visits to US national parks declined by one-quarter during a 24-year period (Soga and Gaston 2016), and visits to public lands or national parks in the US, Japan, and Spain also declined (Pergams and Zaradic 2008). Balmford *et al.* (2009) offered a broader perspective by looking at visitation trends for 280 protected areas across the globe, and reported mixed results; specifically, the authors found positive trends in Africa, Asia, and Latin America, suggesting a possible shift from domestic- to foreign-based EoN in certain high-income countries. Further tracking of park visits at larger scales is needed to better understand current trends. New approaches, such as screening crowd-sourced information shared on social media (Wood *et al.* 2013), may be useful but have yet to be fully developed. For instance, in one study, photo sharing in Flickr was used to track trends in visits to protected

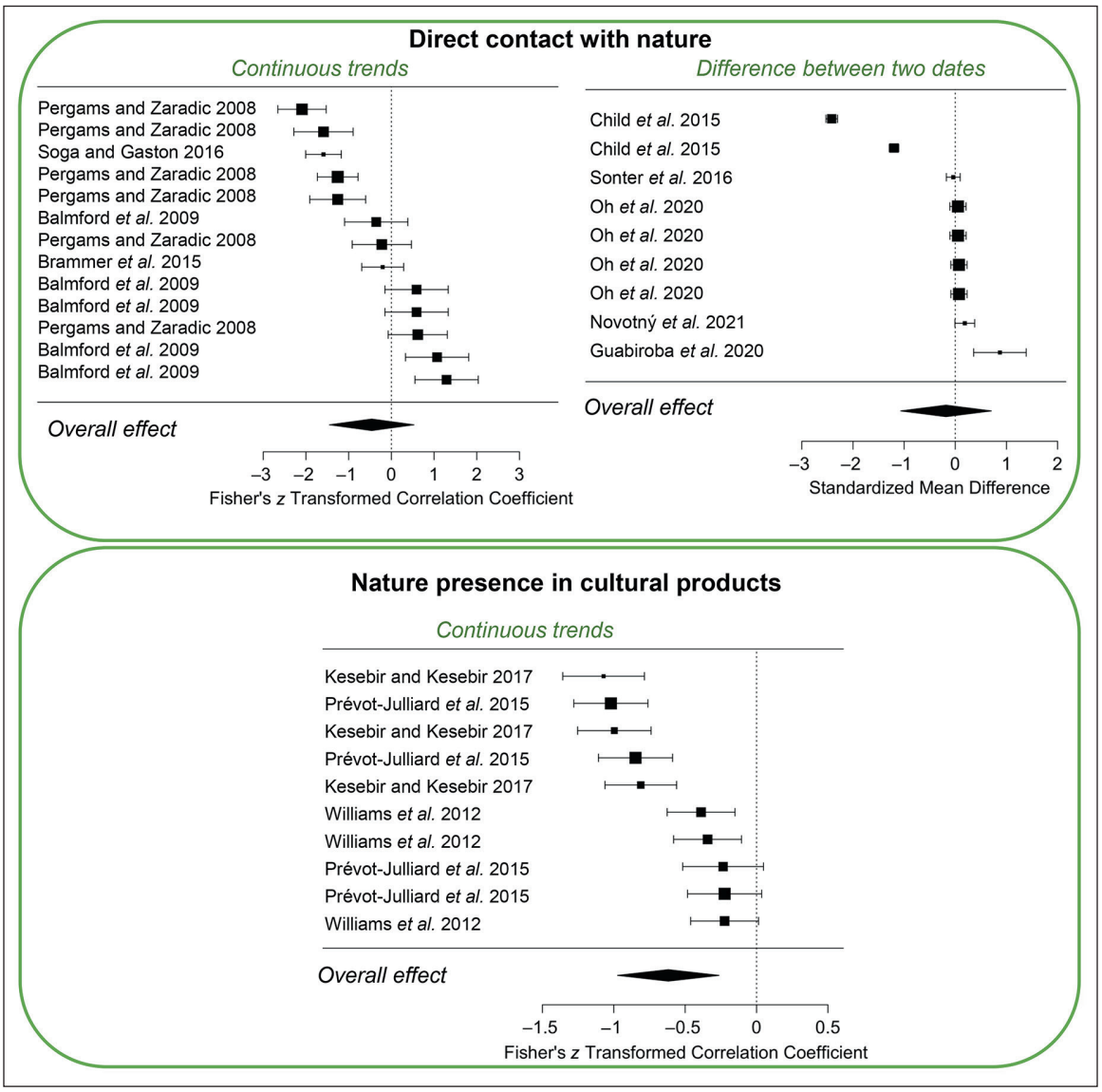

Figure 2. Forest plots from meta-analyses of effect sizes for (top) direct EoN and (bottom) vicarious EoN. Solid squares represent effect sizes (Fisher's *z* for continuous data and standardized mean differences [SMD] for comparisons between two data points) per study. Horizontal lines indicate 95% confidence intervals. For more details, see Panel Figure 2 in WebPanel 1. Note: more than one type of EoN may be described in a single publication.

areas in Vermont over a 7-year period, but no clear trends were discerned (Sonter *et al.* 2016).

With regard to other types of outdoor activities, one survey found no statistically significant trends in the use of greenspaces in Singapore (Oh *et al.* 2020), whereas a long-term survey in Germany and the Czech Republic suggested increased visitation to forests by children (Novotný *et al.* 2021). Certain studies reported declining frequency of participation in various outdoor recreational activities (Soga and Gaston 2016) including camping and hiking in the US (Pergams and Zaradic 2008), while a county-scale study in South Carolina suggested that participation in outdoor physical activities declined among women but increased among men (Child *et al.* 2015). Finally, participation in outdoor skating in Canada was shown to have fallen by 84,000 users per decade, a trend expected to accelerate in the future due to climate change (Brammer *et al.* 2015).

Research by Imai *et al.* (2019) demonstrated a decline in people's nature-based observations of plant and animal taxa in Japan, a trend that was particularly pronounced in children. Similarly, another study in Japan showed that both the frequency and diversity of childhood experiences with local flowering plants decreased over time (Soga *et al.* 2018). In Germany and the Czech Republic, a survey spanning 120 years found no overall trend in EoN among children, with nine EoN metrics in decline (eg observing Eurasian skylark [*Alauda arvensis*]), 16 increasing (eg observing European hedgehog [*Erinaceus europaeus*]), and six for which no clear trend was detected (eg observing cuckoos [*Cuculus canorus*]) (Novotný *et al.* 2021). These types of EoN may be positively affected by citizen-science programs and platforms (eg iNaturalist), which can inspire people to observe wild organisms regardless of where they live, influencing their knowledge

and beliefs (Cosquer *et al.* 2012). However, the rise in popularity of these platforms should not be taken as an unambiguous sign of increasing EoN (for instance, participants may have conducted similar observations before the platform existed). Studies at the individual level are needed to interpret trends in the use of these platforms.

Direct interactions with wildlife also occur in the form of recreational harvesting activities. Participation in these activities appears to be on the decline in the US, with a decrease in recreational fishing and hunting practices in Minnesota (Soga and Gaston 2016) and a decrease in demand for fishing and hunting licenses nationally (Pergams and Zaradic 2008). In contrast, one study reported a rapid increase in recreational fishing in Trinidad, with subsequent negative impacts on local reef fish communities (Guabiroba *et al.* 2020). Sometimes qualified as consumptive (Clayton *et al.* 2017), these forms of EoN may not have the same effect on individuals as non-extractive activities, given that participation in hunting and fishing may promote a sense of domination over nature, which can discourage pro-environmental attitudes (Ghasemi and Kyle 2022). However, another study found that hunting and birdwatching enhanced adoption of conservation behaviors to a similar degree (Cooper *et al.* 2015).

Our results highlight the paucity of research on direct EoN, which impedes the tracking of EoN trends. Taken together, the 11 studies measuring trends in direct EoN that were included in our analysis indicated that although some forms of EoN are clearly decreasing at local scales, general trends are considerably more nuanced than typically assumed (Figure 1). Indeed, our meta-analysis of effect sizes revealed no significant overall trend in direct EoN (overall SMD [differences between two dates]: –0.18; $z = -0.40$, $P = 0.69$) (overall Fisher's z [continuous trends]: –0.46; $z = -0.91$, $P = 0.36$) (Figure 2), with the large uncertainty attributable to the limited sample size. To ensure that the lack of effect was not due to the inclusion of studies of too short a duration for changes in EoN to be observed, we added the number of years between the first and last measure of EoN to our model; however, inclusion of this factor produced no significant change ($z = -0.32$, $P = 0.75$ for continuous trends; $z = 0.32$, $P = 0.75$ for differences between two dates) (see Panel Figure 3 in WebPanel 1).

Vicarious EoN through cultural products

EoN is not restricted to outdoor activities and can involve indirect contact with nature as well (Clayton *et al.* 2017; Gaston and Soga 2020), although this type of EoN may lead to weaker emotional responses because of limited sensory stimulation (Kahn *et al.* 2009; Truong and Clayton 2020). In particular, cultural products (eg books, movies) provide vicarious EoN by exposing people to natural landscapes and activities. As a result, with respect to cultural products, trends in nature presence can serve as a proxy for trends in vicarious EoN (Williams *et al.* 2012), while at the same time provide information about more general trends in societal connections with nature (Prévot-Julliard *et al.* 2015).

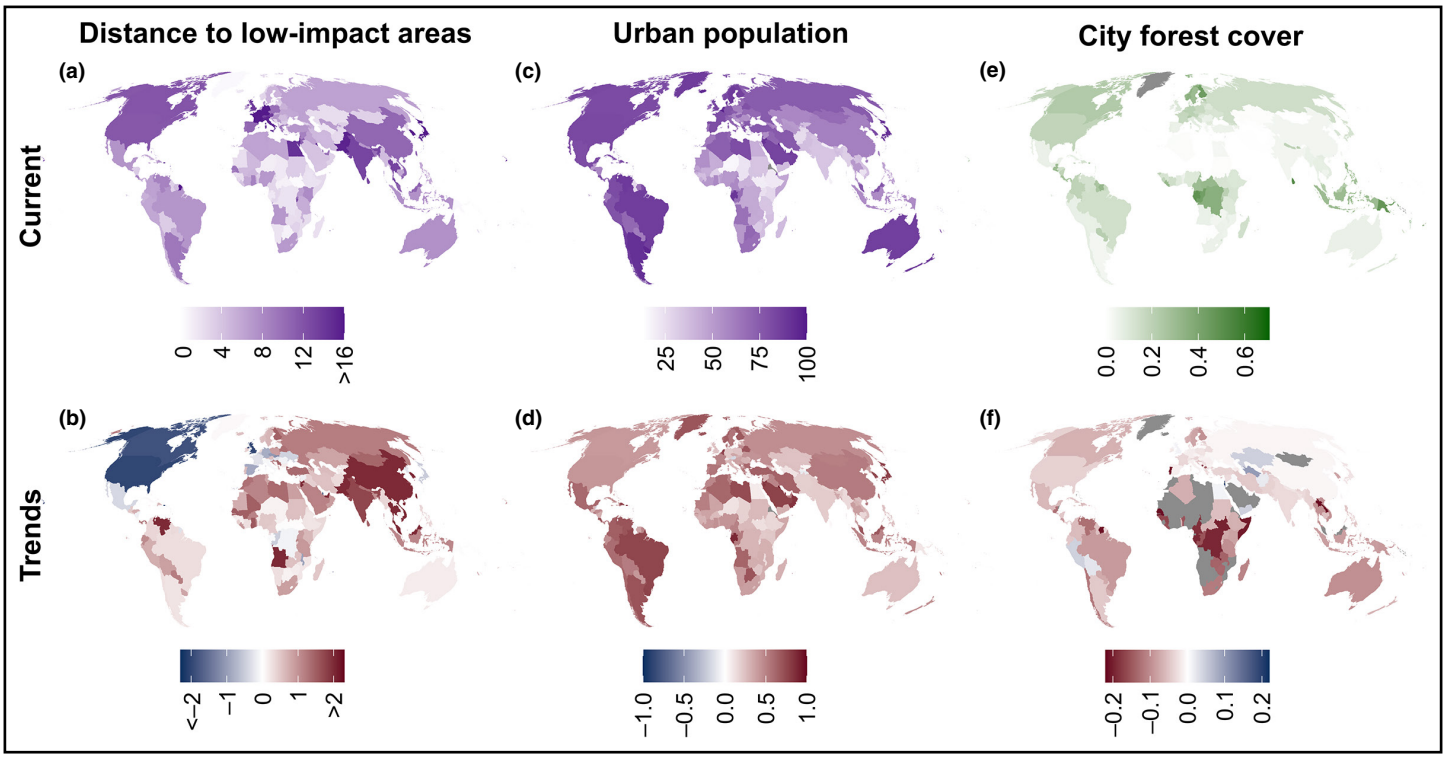

Figure 3. Current values (top row) and trends over time (bottom row) of three global metrics of EoN opportunities (columns). (a and b) Distance to low-impact areas, measured as the average distance between each country's inhabitants and the nearest area with a human footprint below ten. (c and d) Urban population, measured as the proportion of each country's population living in an urban area. (e and f) City forest cover, measured as the proportion of tree cover in cities. Detailed methodologies for each metric calculation are provided in WebPanel 1.

EoN is particularly important for children, as values and concerns about the environment are strongly shaped by early-life experiences (Wells and Lekies 2006; Louv 2008; Chawla 2009), which may also be true for vicarious EoN (Prévot-Julliard *et al.* 2015). Of the seven identified studies measuring trends in nature presence in cultural products, three papers documented declines for children. Both natural settings and the presence of animals declined in children's books in the US from 1938 to 2008, while depictions of built environments became more common over that period (Williams *et al.* 2012); similar results were found for children's books in Australia (Babb *et al.* 2018). Likewise, both the proportion of natural settings and animal species richness decreased over time in Disney and Pixar movies between 1937 and 2010, while portrayals of human-made natural settings appeared to increase (Prévot-Julliard *et al.* 2015). Collectively, these three studies suggest that nature presence in children's cultural products is decreasing, which may affect children's imagination and connection with nature.

Vicarious EoN is also important for adults, however. We identified additional studies that explored trends in the nature presence in other cultural products. The most comprehensive of these was the work of Kesebir and Kesebir (2017), who, in an analysis of a corpus of English popular culture, found that nature-related terms in fiction books, song lyrics, and film storylines have declined significantly since 1950. Similarly, a recent study reported that the abundance and diversity of taxa mentioned in an English creative-literature corpus has declined since the mid-19th century (Langer *et al.* 2021). Tree-related terms have also become less common in written text in the Oxford English Dictionary since 1900 (Wolff *et al.* 1999). In contrast, researchers focusing on advertisements in two Canadian magazines did not detect any clear trends in the representation of outdoor activities (Dearden and Andressen 1987).

Overall, these studies reflect a significant ongoing removal of nature in cultural products (overall Fisher's $z = -0.62$; $z = -3.41$; $P = 0.0007$) (Figure 2). Their temporal scope, when incorporated into our model, did not have a significant effect ($z = 1.54$, $P = 0.12$) (see Panel Figure 3 in WebPanel 1). However, it is important to note that the studies included in our analysis did not evaluate trends in people's vicarious EoN (which could be measured via, for instance, wildlife documentary viewership), highlighting an important research gap. Moreover, it is possible that people engage in vicarious EoN through other sources, such as social media, online videos, or video games (Clayton *et al.* 2017; Truong *et al.* 2018). Further research is needed to better understand trends in vicarious EoN, as well as the influence each type of EoN has on an individual's connection with nature (Truong and Clayton 2020).

Geographical biases in empirical data

Although there is great heterogeneity in trends in EoN, there is no clear spatial structure in the direction of the trends (for example, all positive trends in one continent), and thus we cannot conclude that there is any spatial pattern in the extinction of experience (Figure 1). However, our review did reveal a marked geographical bias in current knowledge about trends in EoN (Figure 1), with North America, Western Europe, and Japan accounting for 61% of the studies, whereas virtually no similar research has been conducted in Latin America, Africa, Asia (except for Japan), and Oceania. Thus, there is no support for the extinction of experience as a global phenomenon, simply because existing evidence is largely limited to a handful of high-income countries.

General trends in EoN opportunities

Although detailed studies are needed to investigate EoN trends in understudied regions, an initial sense of these patterns can be obtained from examining trends in EoN opportunities, which, along with orientation toward engaging with nature, are important drivers of EoN (Soga and Gaston 2016), and have been used in the past as potential evidence to support the extinction of experience principle (eg trends in urban population; Turner *et al.* 2004). At more local scales, the increasing areal extent of urban greenspaces in some cities suggests that new EoN opportunities are being created (albeit not via exposure to true wild nature) (Dallimer *et al.* 2011; Kabisch and Haase 2013; Zhang and Yang 2014). We measured global trends in EoN opportunities in each country by assessing temporal trends in three metrics – distance to low-impact areas, proportion of urban population, and city forest cover – that we suggest are the best-available global proxies for trends in contact with nature (see WebPanel 1 for additional details).

Distance to low-impact areas

We developed a metric that estimates the average distance from where an individual lives to the nearest area with low human impact as a proxy for human accessibility to natural areas. This metric was calculated by combining a map of human population density (CIESIN 2018) with a map of the human footprint (Williams *et al.* 2020), considering pixels with a human footprint below ten to represent a low-impact area. We estimated both the current value of this metric in 2020 and how it trended between 2000 and 2020.

In 2020, humans lived on average 9.73 km away from the nearest low-impact area, with greater distances for people living in Europe, Southeast Asia, and North America (Figure 3a). Conversely, many countries in Africa and central Asia show relatively low distances from low-impact areas. The average distance to low-impact areas has increased by 0.64 km (7%) from 2000 to 2020 across the globe, suggesting a negative trend in EoN opportunities. This trend was found in Asia, Africa, and Latin America (Figure 3b), and was particularly strong in

Angola and the United Arab Emirates, where the average distance to low-impact area increased by 5.8 km and 5.6 km, respectively. In contrast, local contractions in the human footprint have resulted in reducing the distance to low-impact areas in parts of Europe and North America (Venter *et al.* 2016; Williams *et al.* 2020).

Proportion of urban population

A commonly used proxy for EoN opportunities is the proportion of the urban human population, the segment most likely to be disconnected from nature on a day-to-day basis (Turner *et al.* 2004). We used data from the World Bank to map the proportion of the urban population in each country in 2019 and to calculate trends between 1960 and 2019 (World Bank 2021). The proportion of urban population was particularly high in Europe and North America, but also in South America, North Africa, and Australia (Figure 3c). Several countries (eg India) feature a relatively low proportion of urban population but a high average distance to low-impact areas, mainly because of large rural populations living in areas with a high human footprint (Williams *et al.* 2020).

The proportion of urban population increased from 33.6% to 55.7% over the past 60 years, with increasing trends occurring in 92% of countries (Figure 3d), particularly those in South America and North Africa.

City forest cover

Reductions in daily EoN opportunities due to population shifts toward urban areas could be mitigated by greenspace availability, as these can serve as important sources of EoN (Fuller *et al.* 2007; Dallimer *et al.* 2011). This necessitates a better understanding of how greenspaces have changed over the past several decades, but this has only been investigated at the local scale, primarily in Europe (Dallimer *et al.* 2011; Kabisch and Haase 2013) and China (Zhang and Yang 2014).

Here, we calculated the average city forest cover per country (in 2020, and trends between 2000 and 2020) because forests provide important EoN (Williams and Harvey 2001) and because forests have been mapped over time at fine-scale resolution (Hansen *et al.* 2013). Although this metric is not necessarily representative of all greenspaces in cities (for instance, grasslands are not considered), temporal trends in city forest cover offer the best available estimates for trends in EoN opportunities within urban areas.

Countries with the highest city forest cover were mostly located in biomes associated with forest habitats (Figure 3e), in both tropical (South America, Equatorial Africa, Southeast Asia) and northern (Scandinavia, North America) regions. During the past 20 years, however, city forest cover has declined in virtually all of the countries in those regions, especially within Equatorial Africa (Figure 3f). Of the 133 countries containing more than 5% city forest cover in 2000, 125 and 34 experienced declines in city forest cover by >5% and >10%, respectively. Positive trends were found in only eight countries (including Peru and Bolivia, with +4.4% and + 2.4%, respectively), indicating that EoN opportunities are decreasing for the growing urban populations in most regions. Our results are largely consistent with previous smaller scale studies (Dallimer *et al.* 2011; Kabisch and Haase 2013).

Discussion

Here, we present the results of the first systematic review of global trends in EoN, a much-needed effort because many authors assume the extinction of experience as true (Pyle 2003; Miller 2005). When referring to this process, authors often cite case studies or non-systematic reviews, but these approaches do not offer a complete picture. By reviewing the literature systematically and performing a meta-analysis, we provide a more neutral view of current knowledge in EoN trends, although this may also be affected by publication biases.

Perhaps our most striking result was the very low number of studies (n = 18) in which trends in EoN were assessed, suggesting that claims about the extinction of experience may be based on insufficient evidence. It is worth noting, however, that our review focused solely on English-language academic research, and that some relevant studies published in other languages may therefore have been omitted. In addition, our results suggest a more nuanced picture than implied by the hypothesized extinction of experience. While finding evidence for declining trends in both direct EoN and nature presence in cultural products, our analysis also revealed a substantial proportion of studies reporting neutral or even positive trends (Figure 1). As a result, our meta-analysis failed to detect a general trend for direct EoN, highlighting that current evidence remains inadequate to support a global decline in EoN (Figure 2).

Heterogeneity in trends in EoN could stem from variability in the trends of different types of EoN. We uncovered compelling evidence for a decline not only in nature presence in children's cultural products (Williams *et al.* 2012; Prévot-Julliard *et al.* 2015; Babb *et al.* 2018) but also in park visits in the US and Japan (Pergams and Zaradic 2008; Balmford *et al.* 2009; Soga and Gaston 2016), whereas heterogeneous trends were detected for other types of EoN. Moreover, our analyses highlighted that certain activities, such as visiting zoos and playing video games displaying natural items, have not been studied from a temporal perspective, and so it has yet to be confirmed whether they might be on the rise and could provide genuine EoN (Clayton *et al.* 2017; Truong *et al.* 2018; Truong and Clayton 2020). Similarly, a better understanding of the current impact of citizen-science platforms on trends in EoN is needed. Further research is therefore required to monitor trends in the diversity of EoN types (Gaston and Soga 2020)

to improve our understanding of whether EoN is truly in decline or whether some forms of EoN are being replaced by others (Truong and Clayton 2020).

Disentangling which types of EoN are increasing and which are decreasing is also important because different types of EoN may have different effects on individuals. An initial distinction can be made between direct and vicarious types of EoN. While more research is needed on this topic, evidence suggests that direct EoN may have greater impact than vicarious EoN. Experimental comparisons of interactions with nature (eg walks in forests or views of natural scenes) experienced either directly or vicariously showed that vicarious interactions had a reduced impact (if any) on individuals' affect or well-being (Kahn *et al.* 2009; Calogiuri *et al.* 2018). This may be because direct interactions offer more interactive and multisensory forms of EoN, with greater opportunities for random discoveries and interactions (Clayton *et al.* 2017; Truong and Clayton 2020). Another important distinction may be between intentional (eg observing a deer after actively tracking one) and incidental (eg observing a deer on the way home) EoN, as they may have different implications (Russell *et al.* 2013). In particular, intentional EoN may mostly involve people with a relatively high concern for environmental issues, whereas incidental EoN may be more broadly distributed within a population and therefore critical to maintaining connections between people and nature (Beery *et al.* 2017). If – as our results suggest – EoN opportunities are globally declining (Figure 3), then incidental EoN could be decreasing, a trend of critical concern.

Our review revealed a strong geographical bias toward North America, Western Europe, and Japan, leaving a sizeable knowledge gap for much of the world and highlighting an urgent need for additional research. The metrics that we developed, however, indicate a sharp decline in daily EoN opportunities in understudied regions (that is, increasing distance to natural areas, increasingly urban populations, and decreasing forest coverage within cities), one that is occurring more rapidly than in other parts of the world. As proxies for EoN opportunities, these metrics do not provide direct evidence for declines in EoN, because we did not quantify orientation toward nature (Soga and Gaston 2016). However, these metrics clearly demonstrate that the same trends that have been observed in Europe and North America for several decades are now occurring in many other countries, providing a strong signal for a global decline in EoN. Further developing global indices of EoN and EoN opportunities will be important in the near future to monitor trends in human connections with nature more accurately, especially given that the post-2020 Global Biodiversity Framework may include a target on people's access to and benefits from green- and bluespaces (SCBD 2021).

Overall, our analyses indicate that, although many EoN types are likely in global decline, empirical evidence to support the hypothesized extinction of experience is lacking, and that additional research focusing on different types of EoN and different countries is needed to better understand the prevalence and magnitude of this phenomenon. Moreover, quantitative studies that combine different measures and types of EoN are necessary to better predict how changes in EoN can impact human values, norms, and behaviors.

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Data Availability Statement

Data used in the meta-analysis and code used to calculate the indices of EoN opportunities are available at https://doi.org/10.5281/zenodo.5707174.

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FrontiersEcoPics

Between wrinkles and stripes: the enigma of the old centurion

The wrinkle-faced bat (*Centurio senex*) is a rarely captured, frugivorous bat species – which is also a seed predator – distributed across Central America and northern South America. Despite purportedly having the strongest bite force within members of the Phyllostomidae family, little else is known about aspects of this bat's natural history, including which fruits and seeds it prefers.

Among the 226 described species in the Phyllostomidae, *C senex* is unique in appearance, with (as its common name suggests) a wrinkled face and with striped, partly translucent wings. The wrinkles have been hypothesized to help the bat direct juice extracted from fruits into its mouth, or to assist with navigation through echolocation. However, evidence to support either statement has so far not been found.

Wing translucency in bats is associated with camouflage, thermoregulation, and foraging strategies. Yet, for nearly all bat species with translucent wings, that translucency is distributed across the entire wing – except for *C senex* and a few others. In addition, no other known bat species possess wing stripes. The adaptive advantage of both striped wings and partially translucent wings remains a mystery.

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