Exposure to Natural versus Urban Environments: Short-term Effects on Stress, Stress-Related Brain Function, and Hippocampal Structure

Dissertation

zur Erlangung des akademischen Grades
Doktor der Naturwissenschaften (Dr. rer. nat.)

eingereicht am Fachbereich Erziehungswissenschaft und Psychologie
der Freien Universität Berlin

von

Sonja Sudimac

Berlin, Januar 2024

Erstgutachter:

Prof. Dr. Ulman Lindenberger

Max-Planck-Institut für Bildungsforschung, Berlin

Freie Universität Berlin (Honorarprofessor)

Zweitgutachter:

Prof. Dr. Simone Kühn

Max-Planck-Institut für Bildungsforschung, Berlin

Datum der Disputation: 10.06.2024

Acknowledgements

This dissertation was conducted within the Lise Meitner Group for Environmental Neuroscience of the Max Planck Institute for Human Development, Berlin, Germany. During my time as a pre-doctoral student I was a fellow of the International Max Planck Research School on the Life Course (LIFE).

First and foremost, I want to express my gratitude to Prof. Dr. Simone Kühn for providing me with the opportunity to conduct my research. Thank you for your exceptional guidance, invaluable advice, and intellectual inspiration throughout my whole doctoral journey. Without your immense support and dedication, submitting this dissertation today would have not be possible. I would further like to extend my gratitude to Prof. Dr. Ulman Lindenberger for his willingness to serve as my doctoral advisor, for reviewing this thesis and for valuable insights that have enriched this work. I am also thankful to Prof. Dr. Steffi Pohl, Prof. Dr. Simone Grassini, and Dr. Annette Brose for kindly agreeing to be members of my doctoral committee. I also wish to thank Prof. Dr. Carolina de Weerth and Dr. Johanna Drewelies for their collaborative efforts and for generously sharing their knowledge with me.

A special thank you goes to my colleagues and friends from the Lise Meitner Group. Thank you Nour, for your invaluable companionship in this journey, and for constant support and encouragement. Thank you, Maike, for always being attentive and readily offering your help. Thank you, Izabela, Emil, Kira, Moana, Caroline, Elena, Kağan and Kim for all the engaging conversations, the collaborative spirit within our group, and for an inspiring and supporting environment. I also want to thank to my fellows from the LIFE program, Elisa, Sina, and Claire, for always offering a listening ear. I am truly fortunate to have you all as colleagues.

I am very grateful to the research assistants who supported my projects and to participants who generously contributed to my research. I am particularly thankful to everyone who supported me in conducting the WalkOut and InfantWalk study, including Kathi Schmalen, Elena Isenberg, Vera Sale, Mirjam Reidick, Laura Scherliess, Kağan Porsuk, Jordan Elias, Jona Carmon, and to Sonali Beckmann, Nadine Taube, Thomas Feg and Sebastian Schröder on the MRI team. I am also very thankful to Silke Witte, for her invaluable help with administrative matters when it was most crucial.

Finally, I want to express my deepest gratitude to my family. To my grandparents for instilling in a me passion for learning and curiosity for wondering about the world. To my parents and my sister for their unconditional love, encouragement, and unwavering faith in me. Hvala vam na svemu. And to Ezequiel for his endless patience, calmness and support. I am deeply grateful for having you all in my life.

Summary

Mental health care represents a major global health challenge in contemporary societies. The higher frequency of mental health issues in urban, compared to rural areas, gains particular significance in light of the world's rapidly accelerating urbanisation. Therefore, it is essential to understand how urban and natural environments impact our mental and brain health. Research shows that exposure to nature, in comparison to exposure to urban environments, improves mood, reduces stress, as well as physiological indicators of stress. Yet, the neural mechanisms behind the effects of natural and urban environments are not well understood. First studies have indicated that living environments are associated with mental health, as well as with brain function and structure. However, due to the inherent limitations of cross-sectional studies, the causal relationship between physical environments and brain health remains unestablished.

This dissertation consists of four publications investigating the short-term causal effects of exposure to natural and urban environments on stress, stress-related brain function and hippocampal structure.

In *Paper I* (Sudimac et al., 2022) we examined effects of a one-hour walk in a natural versus urban environment on stress-related brain function. The results indicated that activity in the amygdala, a brain region associated with stress, decreased after the nature walk, whereas no significant change was noted after the urban walk. The findings suggest that exposure to nature may have beneficial effects on stress-related brain regions, potentially acting as a preventive measure against stress-related mental health issues.

In *Paper II* (Sudimac & Kühn, 2022) we explored sex differences in the impact of a one-hour walk in a natural versus urban environment on amygdala activity. Our results revealed a decrease in amygdala activity following the nature walk exclusively in women, with no significant change observed in men. This outcome indicates that women may benefit more from exposure to natural environments and underscores the necessity of considering individual differences, like sex, in the neural responses to exposure to natural and urban environments.

In *Paper III* (Sudimac & Kühn, 2024) we investigated the impact of a one-hour walk in a natural versus urban environment on the structure of the hippocampus. We observed an increase in the volume of the hippocampal subfield, subiculum, following the nature walk, while no significant change was observed after the urban walk (though the interaction did not withstand the Bonferroni correction). Since the subiculum plays a role in dampening the stress

response via the hypothalamic-pituitary-adrenal axis, our findings suggest that exposure to nature might positively influence a brain region associated with inhibition of stress response.

In *Paper IV* (Sudimac et al., 2024) we assessed the effects of a walk in residential natural versus urban environments on subjective and physiological indicators of stress in mothers and their infants. We found no significant differences between exposure to natural and urban environments in mothers' self-reported stress or in the stress-related cortisol levels, in both mothers and infants. However, a reduction in cortisol in mothers and infants was observed after walks in both natural and urban environments, indicating that the act of walking in residential areas might have a calming effect, regardless of the environment.

In summary, this dissertation reveals a seminal evidence for the potential benefits of short-term exposure to natural relative to urban environments on stress-related brain function and brain structure. Furthermore, it emphasizes the need to consider individual differences, like sex and age, in exploration of natural and urban environments on mental and brain health. In conclusion, this work contributes to the growing body of research on environmental neuroscience and has potential implications for urban planning and public health strategies aimed at mitigating stress and enhancing mental health in urban populations.

Zusammenfassung

Die psychische Gesund stellt eine bedeutende globale Herausforderung in der heutigen Gesellschaft dar. Die höhere Häufigkeit psychischer Probleme in städtischen im Vergleich zu ländlichen Gebieten gewinnt besonders an Bedeutung angesichts der weltweit schnell fortschreitenden Urbanisierung. Daher ist wichtig zu verstehen, wie städtische und natürliche Umgebungen unsere psychische und Gehirngesundheit beeinflussen. Forschungen zeigen, dass der Kontakt mit Natur, im Vergleich zur Exposition gegenüber städtischen Umgebungen, die Stimmung verbessert, Stress sowie physiologische Stressindikatoren reduziert. Die neuronalen Mechanismen hinter den Auswirkungen natürlicher und städtischer Umgebungen sind jedoch noch nicht gut verstanden. Erste Studien weisen darauf hin, dass Wohnumgebungen mit psychischer Gesundheit sowie mit Gehirnfunktion und -struktur zusammenhängen. Allerdings blieben, aufgrund der inhärenten Einschränkungen von Querschnittsstudien, die kausalen Beziehungen zwischen physischen Umgebungen und Gehirngesundheit ungeklärt.

Diese Dissertation besteht aus vier Veröffentlichungen, in denen die kurzfristigen kausalen Auswirkungen der Exposition gegenüber natürlichen und städtischen Umgebungen auf Stress, stressbezogene Gehirnfunktion, und die Struktur des Hippocampus untersucht werden.

In *Papier I* (Sudimac et al., 2022) untersuchten wir die Auswirkungen eines einstündigen Spaziergangs in einer natürlichen im Vergleich zu einer städtischen Umgebung auf stressbezogene Gehirnfunktionen. Die Ergebnisse zeigten, dass die Aktivität in der Amygdala, einer mit Stress assoziierten Gehirnregion, nach dem Spaziergang in der Natur abnahm, während nach dem städtischen Spaziergang keine signifikante Veränderung festgestellt wurde. Die Befunde legen nahe, dass die Exposition gegenüber der Natur positive Auswirkungen auf stressbezogene Gehirnregionen haben könnte und somit als präventive Maßnahme gegen stressbedingte psychische Gesundheitsprobleme wirksam sein könnte.

In *Paper II* (Sudimac & Kühn, 2022) erforschten wir Geschlechtsunterschiede in der Wirkung eines einstündigen Spaziergangs in einer natürlichen im Vergleich zu einer städtischen Umgebung auf die Amygdala-Aktivität. Unsere Ergebnisse zeigten eine Abnahme der Amygdala-Aktivität nach dem Natur-Spaziergang ausschließlich bei Frauen, bei Männern wurde keine signifikante Veränderung beobachtet. Dieses Ergebnis deutet darauf hin, dass Frauen möglicherweise stärker von der Exposition gegenüber natürlichen Umgebungen profitieren und unterstreicht die Notwendigkeit, individuelle Unterschiede wie Geschlecht in

den neuralen Reaktionen auf die Exposition gegenüber natürlichen und städtischen Umgebungen zu berücksichtigen.

In *Paper III* (Sudimac & Kühn, 2024) untersuchten wir die Auswirkungen eines einstündigen Spaziergangs in einer natürlichen im Vergleich zu einer städtischen Umgebung auf die Struktur des Hippokampus. Wir beobachteten eine Zunahme des Volumens des hippokampalen Subfeldes, Subikulum, nach dem Natur-Spaziergang, während nach dem städtischen Spaziergang keine signifikante Veränderung festgestellt wurde (obwohl die Interaktion nach Anwendung der Bonferroni-Korrektur nicht signifikant war). Da das Subikulum eine Rolle bei der Dämpfung der Stressreaktion über die hypothalamisch-hypophysär-adrenale Achse spielt, legen unsere Ergebnisse nahe, dass die Exposition gegenüber der Natur einen positiven Einfluss auf eine mit der Hemmung der Stressreaktion assoziierte Gehirnregion haben könnte.

In *Paper IV* (Sudimac et al., 2024) bewerteten wir die Auswirkungen eines Spaziergangs in natürlichen im Vergleich zu städtischen Wohngebieten auf subjektive und physiologische Stressindikatoren bei Müttern und ihren Säuglingen. Wir fanden keine signifikanten Unterschiede zwischen der Exposition gegenüber natürlichen und städtischen Umgebungen in Bezug auf selbstberichteten Stress der Mütter oder auf die Cortisolwerte, Stresshormon, sowohl bei Müttern als auch bei Säuglingen. Allerdings wurde eine Reduzierung des Cortisols bei Müttern und Säuglingen nach Spaziergängen in beiden Umgebungen beobachtet, was darauf hinweist, dass das Spazierengehen in Wohngebieten unabhängig von der Umgebung eine beruhigende Wirkung haben könnte.

Zusammenfassend zeigt diese Dissertation bahnbrechende Hinweise für die potenziellen Vorteile einer kurzfristigen Exposition gegenüber natürlichen im Vergleich zu städtischen Umgebungen auf stressbezogene Gehirnfunktion und -struktur. Weiterhin betont sie die Notwendigkeit, individuelle Unterschiede wie Geschlecht und Alter bei der Erforschung natürlicher und städtischer Umgebungen auf die psychische und Gehirngesundheit zu berücksichtigen. Abschließend trägt diese Arbeit zur wachsenden Forschung im Bereich der Umweltneurowissenschaften bei und könnte Implikationen für die Stadtplanung und öffentliche Gesundheitsstrategien haben, die darauf abzielen, Stress zu mildern und die psychische Gesundheit in städtischen Bevölkerungen zu verbessern.

List of included papers

This doctoral dissertation incorporates the following four original papers:

Paper I

Sudimac, S., Sale, V., & Kühn, S. (2022). How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature. *Molecular Psychiatry*, *27*(11), 4446–4452. https://doi.org/10.1038/s41380-022-01720-6

Paper II

Sudimac, S., & Kühn, S. (2022). A one-hour walk in nature reduces amygdala activity in women, but not in men. *Frontiers in Psychology*, *13,* 1–13. https://doi.org/10.3389/fpsyg.2022.931905

Paper III

Sudimac, S., & Kühn, S. (2024). *Can a nature walk change your brain? Investigating hippocampal brain plasticity after one hour in a forest.* PsyArXiv. https://doi.org/10.31234/osf.io/g64bq [Manuscript under revision]

Paper IV

Sudimac, S., Drewelies, J., De Weerth C.* & Kühn, S.* (2024). *Effects of a walk in a residential natural vs. urban environment on objective and subjective stress indicators in mothers and their infants.* PsyArXiv. https://doi.org/10.31234/osf.io/pz83m [Manuscript under revision]

* These authors share last authorship.

List of abbreviations

ACC	Anterior Cingulate Cortex
ART	Attention Restoration Theory
CBT	Cognitive Behavioural Therapy
CRT	Condition Restoration Theory
dlPFC	dorsolateral Prefrontal Cortex
EEG	Electroencephalography
FFT	Fearful Faces Task
fMRI	functional Magnetic Resonance Imaging
HPA	Hypothalamic–Pituitary–Adrenal
MIST	Montreal Imaging Stress Task
MRI	Magnetic Resonance Imaging
NBRT	Nature-Based Biopsychosocial Resilience Theory
pACC	perigenual Anterior Cingulate Cortex
PFA	Perceptual Fluency Account
sACC	subgenual Anterior Cingulate Cortex
sgPFC	subgenual Prefrontal Cortex
SRT	Stress Reduction Theory
vmPFC	ventromedial Prefrontal Cortex
VR	Virtual Reality
WEIRD	Western, Educated, Industrialised, Rich, Democratic

Contents

1 General theoretical and empirical background

Currently, we are witnessing an unprecedented level of urbanisation. To date, 55% of the world population resides in cities, a figure that is projected to increase to 68% by 2050 (United Nations, Department of Economic and Social Affairs, Population Division, 2019). Given a higher incidence of mental disorders in urban compared to rural areas (Peen et al., 2010), this rapid urbanisation underscores the need to examine the effects of urban environments on citizens' well-being. Therefore, research is increasingly focused on understanding the impact of the physical environment on mental health and the brain, as well as on identifying strategies to mitigate these effects and improve the quality of life. While physical environmental factors include pollution, temperature, humidity, and population density (Liu et al., 2023) in this dissertation the term "physical environment" specifically refers to natural and urban environments. This chapter provides an overview of existing research, exploring how natural and urban environments can affect mental health indicators like mood and stress, and their effects on the brain.

1.1 The associations between the physical environment and mental health

Urban settings offer numerous benefits, including improved access to healthcare and education, greater employment opportunities, and cultural enrichment (Dye, 2008; Glaeser, 2011). However, numerous studies have highlighted the potential negative impact of urban living on mental health. There is a growing concern about mental health issues in cities, with a notably higher incidence of mental disorders like mood and anxiety disorders, depression, and schizophrenia in urban compared to rural areas (Peen et al., 2010; Pignon et al., 2023; Purtle et al., 2019; Van Os et al., 2010; Vassos et al., 2012).

According to so-called *drift hypothesis*, higher incidence of mental disorders in cities can be attributed to selective migration (Harriss & Hawton, 2011). That is, individuals more prone to developing disorders may migrate to urban areas, for instance, due to enhanced access to health and social services. However, many studies support the alternative *breeder hypothesis* indicating that the disparities between urban and rural mental health arise primarily from environmental factors. Notably, a longitudinal study demonstrated that individuals who moved to a greener area experienced enhanced mental well-being in the three subsequent years (Alcock et al., 2014). Moreover, a 10-year longitudinal study, which involved over 2 million participants, showed that exposure to natural environments was linked to a lower incidence of mental disorders (Geary et al., 2023).

While the psychiatric literature has been focused on relating mental disorders with adverse factors within urban environments, such as air pollution and traffic noise (Gruebner et al., 2017; Krabbendam et al., 2021), research in environmental psychology has emphasised the positive impacts of nature on well-being (Kühn et al., 2021; Russell et al., 2013). This research suggests that natural environments could potentially mitigate the unfavourable impacts of urban environments (M. Van den Berg et al., 2015). Studies in environmental psychology have consistently highlighted the health benefits of exposure to natural environments in comparison to urban environments, such as enhanced mental health, more physical activity, and a lower risk for several mental disorders (Bratman et al., 2019; Rojas-Rueda et al., 2019; World Health Organization, 2016).

Further evidence reveals a positive link between mental health and residing near natural spaces. There is a consistent positive association between mental health and living near green spaces and coastlines, even when variables like socio-economic factors are taken into account (Callaghan et al., 2021; Garrett et al., 2019; Sturm & Cohen, 2014; White et al., 2021). Moreover, there is a dose-response relationship between the extent of public green spaces and mental well-being: the larger the areas of public green spaces, the better the mental health of the residents tends to be (Wood et al., 2017). Additionally, daily commutes through natural settings have been associated with improved mental health outcomes, in contrast to commutes without natural features (Zijlema et al., 2018). Residing in a neighbourhood rich in green spaces has been identified as a protective factor against the onset of mental disorders. It has been repeatedly shown that living close to green spaces is related to reduced risk for developing depression, as well as other mental disorders (Cohen-Cline et al., 2015; Gascon et al., 2015; Sarkar et al., 2018; M. Van den Berg et al., 2015). Furthermore, high levels of residential green space in childhood have been associated with a reduced likelihood of experiencing a range of mental disorders (Engemann et al., 2019). Interestingly, living close to nature may also be beneficial for physiological indicators of stress. For instance, individuals residing in greener areas were found to exhibit reduced levels of the stress hormone cortisol (Gidlow, Randall, et al., 2016). Since not only proximity to urban parks, but also number of visits to them has been positively associated with mental health (Sturm & Cohen, 2014), it is likely that those living near urban parks will visit them more often, thereby benefiting from their salutogenic effect on mental health. This is supported by a recent study using data from 18 countries that revealed that recreational visits to both green spaces and blue spaces (like lakes or the sea) over the past month were positively associated with increased well-being and inversely related to mental distress (White et al., 2021). While the association between residing near or frequenting green spaces and mental health benefits has been often validated, it is not yet clear why nature is salutogenic for human well-being. Multiple theoretical frameworks in environmental psychology explore the factors behind the human preference for nature and its positive impact on our well-being, and these frameworks will be outlined in the following section.

1.2 Theoretical frameworks

Throughout history, nature has been universally revered for its positive impact on human well-being. Nature is broadly defined as "all the animals, plants, rocks, etc. in the world and all the features, forces, and processes that happen or exist independently of people, such as the weather, the sea, mountains, the production of young animals and growth" (https://dictionary.cambridge.org/dictionary/english/nature). This section will present various theoretical frameworks that propose different approaches to understanding consistently observed positive impacts of nature on mental health and cognition.

The *biophilia hypothesis*, derived from the Greek words "bios" (life) and "philia" (fondness or attraction), proposes that humans have an innate affinity for the natural world. Proposed by Edward O. Wilson (1986), this hypothesis posits that humans are predisposed to be attracted to nature due to our evolutionary history. Our ancestors, reliant on nature for survival essentials like food and shelter, developed an inherent inclination towards nature. This preference for nature emerged as a key trait selected through evolutionary processes across numerous generations, since nature was a reliable source of essential resources. Thus, according to the biophilia hypothesis, our inherent draw to nature and its beneficial impact on our well-being are rooted in our evolutionary history.

*Stress Reduction Theory (SRT)***,** another evolutionary theory, posits that, when in contact with nature, humans experience a rapid, immediate positive psychophysiological response to it (Ulrich, 1983; Ulrich et al., 1991). According to SRT, artificial settings can lead to increased stress levels, whereas nature alleviates stress. This is because humans have a genetically ingrained positive response to nature, a trait developed over millions of years of evolution. Therefore, humans' preference for natural environments is innate. A positive affective response is triggered by specific environmental features, like complexity, structural features (e.g., asymmetry), and absence of threat. Upon encountering these natural features, there is a rapid increase in positive affective response and a concurrent decrease in arousal levels, initiating a restorative process. SRT also states that the calming effects of nature on an individual are more effective if the individual is in a stressed state. Thus, SRT suggests that a reduction in stress levels in natural environments occurs automatically, reflecting our deep evolutionary connection with nature.

Attention Restoration Theory (ART) posits that nature is an ideal place to restore diminished attentional capacity (Kaplan 1995). ART proposes that during our everyday activities (working, studying etc.), voluntary attention is activated and, over time, limited resources of voluntary attention are drained, which leads to mental fatigue. However, nature has the capability of "recharging" our attentional capacity by inducing involuntary attention, while allowing voluntary attention to recover. ART postulates that nature is full of simple elements, such as a breeze of wind or a sound of a river, that evoke "soft fascination", during which drained voluntary attention can be restored. While SRT focuses on quick and innate emotional response to nature, ART highlights slower cognitive processes in contact with nature. In contrast to SRT, ART posits that engagement with nature initially induces restorative processes, that consequently lead to a decrease in stress. ART and SRT should not be viewed as opposing, but rather as complementary theoretical frameworks (Berto, 2014; Joye & Van Den Berg, 2018). They each focus on different aspects of nature's salutogenic effects: ART on the cognitive and SRT on the affective responses.

In addition to SRT and ART, which are the main theoretical frameworks regarding nature's positive effects on mental health, three novel theories have emerged in recent years. The *Perceptual Fluency Account (PFA)* aims to integrate SRT and ART by proposing that natural environments possesses a higher perceptual fluency compared to urban settings, leading to enhanced restorative effects (Joye & Van Den Berg, 2018). PFA suggests that nature's fluency stems from our visual system's inherent tuning to the structure of natural environments as opposed to man-made environments. Specifically, fractal shapes, which are more present in natural environments, are processed more effortlessly than the shapes typically found in urban settings.

Condition Restoration Theory (CRT) proposes that restoration in natural environments results from restorative conditioning (Egner et al., 2020). This process involves associating relaxing experiences previously encountered in nature with nature itself. In contemporary societies, where nature is often a setting for leisure, positive emotions experienced in natural settings become classically conditioned and linked to subsequent nature encounters, leading to restoration in natural environments. Thus, CRT posits that restoration is not inherently tied to the characteristics of nature and can also occur in non-natural environments, indicating that the restorative effect is related to conditioned response than to the environment itself.

Recently, the *Nature-based Biopsychosocial Resilience Theory (NBRT)* was proposed by White and colleagues (2023), suggesting that individuals are consistently faced with a range of environmental, socio-economic, and personal stressors that can disrupt their natural balance, negatively influencing their mental health. However, according to the NBRT, individuals also have a stockpile of biological, psychological, and social resources that they can leverage to counteract the effects of these stressors on their well-being. This resilience can be viewed as a dynamic process that helps to prevent or reduce stress, respond to immediate challenges, and recover from disturbances. NBRT posits that nature plays a pivotal role in maintaining and restoring these resilience resources. The natural environment, with its diverse ecosystems, settings, and elements, offers varied contact experiences that can enhance resilience in stressful situations. Furthermore, the process of responding to stress can indirectly reinforce resilience by fostering behaviours such as increased engagement with natural surroundings.

1.3 Effects of natural and urban environments on mental health

While a substantial body of research have demonstrated a positive correlation between living near natural environments and improved mental health (Callaghan et al., 2021; Cohen-Cline et al., 2015; Engemann et al., 2019; Garrett et al., 2019; Sturm & Cohen, 2014; White et al., 2021; Wood et al., 2017), the cross-sectional nature of these studies prevents the assumption of a causal relationship. To investigate the potential causal relationship between natural and urban environments and mental health, numerous studies have implemented experimental designs in laboratory settings. These studies focused on mental health indicators such as mood and stress.

In these experiments, participants' mental health indicators were measured while viewing photos of either natural or urban scenes, and revealed that merely viewing natural environments can have a positive impact on mood and stress. Specifically, participants reported feeling more relaxed after viewing photos of forests (Song et al., 2018) and experienced reduced feelings of anxiety, hostility, and fatigue after viewing garden images, as compared to urban scenes (Lee, 2017). To enhance the experience of nature immersion, Wang and colleagues (2016) used video footage of natural settings and observed that the natural scenes reduced stress and promoted feelings of restoration, whereas urban scenes elicited negative emotions. Given the complexities of replicating the natural environment within a laboratory setting, much of this research has prioritised visual stimuli, examining the effects of images and videos on mental health. Nevertheless, studies investigating other sensory modalities, such as sounds of nature, have yielded comparable findings. For instance, natural sounds such as the gushing of a water fountain or birdsong have been shown to be more preferred than urban noises (Coensel et al., 2011) and are also effective in improving mood (Benfield et al., 2014). Additionally, listening to birdsong alleviated anxiety and state paranoia, whereas traffic noise increased depressive symptoms in healthy participants (Stobbe et al., 2022).

Given the limitations of two-dimensional photos as a static and sometimes constrained representation of nature, researchers have turned to virtual reality (VR) for a more immersive and realistic experience. With advancements in VR technology, it has become possible to recreate both natural and urban environments in order to provide a more realistic experience of these environments. Thus, studies have found that when nature scenes are presented in immersive VR settings, participants likewise showed a decrease in stress and an increase in positive affect (Mostajeran et al., 2023; Reese et al., 2022). Additionally, these studies showed enhanced perceptions of restorativeness (Mostajeran et al., 2023) and improvements in cognitive performance (Berto, 2014) within these simulated natural settings. Recent reviews examining the impact of VR-based nature experiences (H. Li et al., 2021; Riches et al., 2021) report that most of the studies showed restorative effects, mood improvements and an increase in relaxation and stress recovery, as well as improved cognition after watching natural scenes in VR. However, these reviews also highlight potential methodological concerns in some studies, such as the novelty bias, referring to the possibility that observed effects might stem from the novelty of the VR experience itself, rather than from the natural environment being portrayed (H. Li et al., 2021; Riches et al., 2021).

Furthermore, the ecological validity of above described studies may be called into question, as viewing photos of nature on a screen or in a VR setting may not truly reflect the genuine experience of physically being in a natural environment. Nevertheless, a substantial body of research in environmental psychology has demonstrated the benefits of direct, in situ exposure to nature on mental health. Thus, several reviews exploring the effects of exposure to in situ nature on mental health consistently indicate that such exposure improves mood and reduces stress (Barnes et al., 2019; Corazon et al., 2019; M. M. Hansen et al., 2017; Kondo et al., 2018; Kotera et al., 2022; McMahan & Estes, 2015; Oh et al., 2017). For example, it has been shown that an intervention involving 20 minutes of sitting in a natural setting, as opposed to an urban one, led to reduced stress levels (Beil & Hanes, 2013). Similarly, engaging in outdoor gardening has been shown to decrease stress and improve mood (A. E. Van den Berg & Custers, 2011). Nevertheless, the most common intervention, when it comes to a real-world exposure to nature, is taking a walk in the nature, as this represents the most ecologically valid and typical form of interaction that people have with natural environments. Research on exposure to in situ nature varies very much in terms of the duration of the intervention (Kondo et al., 2018; Oh et al., 2017). Some studies have shown the benefits of brief exposures to nature. For example, a mere 15-minute nature walk, compared to an urban walk, has been demonstrated to enhance positive emotions and attention restoration, while reducing negative emotions and anxiety (Bielinis et al., 2018; Song, Ikei, Igarashi, et al., 2015). On the other hand, interventions can also involve longer visits to a natural environment. For example, mental well-being of university students improved after visiting the university's arboretum for two hours daily over a period of five consecutive weeks (Vujcic and Tomicevic-Dubljevic 2018). Similarly, employees who took nature walks during their lunch breaks twice a week for 8 weeks exhibited improved mental health (Brown et al., 2014).

Exposure to real-world nature has been examined across various natural settings. In Japan, a considerable amount of research has explored the impact of forest environments on mental health within the practice known as *shinrin yoku* or "forest bathing" (M. M. Hansen et al., 2017; Oh et al., 2017). This practice, long appreciated in Japan, entails a mindful immersion in the forest, while engaging all the senses. The term "forest bathing" was officially introduced by the Japanese Forestry Agency in 1982 (M. M. Hansen et al., 2017; Rajoo et al., 2020). The practice involves walking or sitting in a forest, but also interaction with other senses, such as touching and smelling trees and flowers. Today, it is widely embraced activity in Japan, practiced both by the healthy population, but also within clinical settings. Numerous studies highlight the restorative effects of "forest bathing" on mental health (Barnes et al., 2019; Kotera et al., 2022; Oh et al., 2017). For instance, spending one day in a forest has been associated with a more pronounced reduction in negative emotions and increased positive feelings and restoration, compared with time spent in urban settings (Ochiai et al., 2015; Takayama et al., 2014). Similarly, extended stays of two days in a forest have yielded reductions in negative affect, mood improvement, and higher restoration (G. X. Mao et al., 2012). Furthermore, a wide-scale study conducted across 14 forests in Japan showed that spending a day in a forest positively affected participants' mental health, by decreasing anxiety and depression symptoms, and increasing vigor, compared to being in 14 different urban environments (B.-J. Park et al., 2011). Beyond the beneficial effects of forest, urban green spaces, such as urban parks, have been shown to beneficially affect mental health. For instance, previous research indicates that a mere 30-min walk in an urban park, as opposed to a walk in an urban street, can decrease rumination and negative affect, and improve mood (Grazuleviciene et al., 2016; Lopes et al., 2020). Furthermore, research has expanded to include blue spaces (areas adjacent to bodies of water), underscoring their distinct mental health benefits (White et al., 2021). For example, it was found that a walk on a beach by the sea improved mood and decreased stress (Triguero-Mas et al., 2017), whereas walking along a canal was associated with greater restorative experiences than urban walks (Gidlow, Jones, et al., 2016).

The studies showing beneficial effects of being in nature on mental health have also shed light on the therapeutic practice of being in nature, revealing its benefits for both healthy individuals and clinical populations (Kotera et al., 2022). While exposure to nature has been shown to significantly improve overall well-being, it particularly benefits individuals prone to depressive tendencies or those dealing with chronic stress (Furuyashiki et al. 2019; Morita et al. 2007). Thus, taking a walk in nature, compared to a walk in an urban setting, improved mood and cognition in patients with depression (Berman et al., 2012). Furthermore, a 4-week Cognitive Behavioural Therapy (CBT) psychotherapy program conducted in a forest setting resulted in a higher rate of depression remission compared to similar interventions in a hospital or control group (Kim et al. 2009). Additionally, individuals suffering from alcoholism experienced a reduction in depression symptoms after engaging in forest-based interventions compared to a control group (Shin et al., 2011). These findings underscore the therapeutic potential of nature immersion for enhancing mental health, particularly in individuals confronting psychological challenges. Nature-based activities are increasingly being accepted as a therapeutic intervention for people who are at risk for developing a mental disorder. However, it is important to note that while the existing research suggests promising benefits of exposure to nature for mental health, prescribing nature as a therapy, so-called “green prescription”, still needs further investigation before it is widely implemented into everyday health care practice (Adewuyi et al., 2023).

In sum, various approaches involving natural and urban environments, such as photographs, environments simulated in VR, and in situ experiences, have all demonstrated beneficial effects of nature on mental health, particularly in terms of stress and mood, as measured through self-reports. The next section will delve deeper into the physiological evidence that illustrates how natural and urban environments specifically influences one aspect of mental health: stress.

1.4 Effects of natural and urban environments on physiological indicators of stress

The stress-reducing effects of nature are observed not only in self-reported measures but also in physiological indicators of stress. Initial experiments assessing physiological stress markers involved participants viewing photographs of natural and urban environments in laboratory settings. Thus, results showed that viewing photographs of natural landscapes reduced stress-related electrodermal activity compared to viewing photographs of urban roadway (Wang et al., 2016). In an immersive experiment, participants experienced 360-degree nature images while also being exposed to natural scents. This not only lowered perceived stress but also decreased electrodermal stress activity (Hedblom et al., 2019). A recent review focusing on VR representations of natural scenes found that the combination of audio-visual elements from nature in immersive VR setting induced stress recovery, indicated by physiological stress markers (Riches et al., 2021).

To assess physiological stress markers in natural and urban environments in situ, numerous studies have recorded physiological markers during a walk in these settings. Research focused on "forest bathing" has highlighted how the therapeutic effects of forest can enhance the adaptive nervous system's response to stressors. For instance, it has been repeatedly shown that participants who have been exposed to nature exhibit lower levels of the stress hormone cortisol compared to those exposed to an urban environment (Antonelli et al., 2019; Chang et al., 2019; Ewert & Chang, 2018; Gidlow, Jones, et al., 2016; Grazuleviciene et al., 2016; Ochiai et al., 2015; Tsunetsugu et al., 2007). Remarkably, these benefits seem to manifest even after a 15-minute walk in a forest (Kobayashi et al., 2019). Furthermore, "forest bathing" has been found to suppress stress-induced sympathetic activity and increase relaxation-linked parasympathetic activity (Kobayashi et al., 2012; Lee et al., 2014; B. J. Park et al., 2010; Triguero-Mas et al., 2017). The findings have consistently revealed that spending time in forest can decrease heart rate (Ochiai et al., 2015; Song, Ikei, Kobayashi, et al., 2015) and blood pressure and have a positive effect on cardiovascular health (Furuyashiki et al., 2019; Rajoo et al., 2020). Immersion into a forest has also been shown to boost the count of natural killer cells and anticancer proteins (Q. Li et al., 2007). Furthermore, a study showed that elderly individuals with hypertension experienced not only enhanced mood but also reduced blood pressure after a week-long forest immersion, unlike a control group in an urban setting. (G.-X. Mao et al., 2012). Even though extensive research on the effect of "forest bathing" indicates that this practice beneficially affects well-being as well as the cardiovascular system, it is important to note that many of these studies come with limitations. Issues like small sample sizes, non-randomised participant allocation, potentially non-representative samples, and non-blinded participants result in a medium to high risk of bias in these studies (Kotera et al., 2022; Oh et al., 2017).

Even though the benefits of nature for mental health, including mood and stress, have been consistently demonstrated, the underlying neural mechanisms remain largely unexplored. The next section will present the literature that has explored the relationship between the natural and urban environments and brain structure and function.

1.5 Natural and urban environments and the brain

In this section, we provide an overview of existing research that investigates the relationship between natural and urban environments and the brain, starting with an examination of their association with brain structure, and then exploring their correlation with brain function.

1.5.1 Natural and urban environments and brain structure

Recent cross-sectional studies have investigated the association between brain structure and the physical environment. They have revealed a positive correlation between being raised in urban areas or living near green spaces and brain structural health metrics, such as gray matter volume and cortical thickness (Crous-Bou et al., 2020; Haddad et al., 2015; Lammeyer et al., 2019). Thus, a seminal study demonstrated a negative correlation between growing up in an urban environment and the gray matter volume in the dorsolateral prefrontal cortex (dlPFC) (Haddad et al., 2015). Similarly, a study by Lammeyer and colleagues (2019) confirmed the inverse correlation between early-life urbanicity and the gray matter volume in the dlPFC, as well as in the right inferior parietal lobe. As dysfunctions of these regions have been linked to stressful life events (S. N. Kim et al., 2013; Tomoda et al., 2009), and structural and functional alterations of the dlPFC have been found in patients with schizophrenia (Smucny et al., 2022), these findings may suggest a potential mechanism by which an urban upbringing may affect the risk for developing schizophrenia (Haddad et al., 2015; Lammeyer et al., 2019). Furthermore, urban upbringing has been negatively associated with cortical thickness in the left dlPFC, bilateral medial prefrontal cortex, left superior temporal cortex, and left parahippocampal cortex, which are also implicated in schizophrenia (Besteher et al., 2017). A study focusing on the hippocampal formation found that adolescents brought up in exclusively rural environments exhibited a larger left hippocampal formation than those raised exclusively in urban environments, suggesting a potential beneficial effect of natural environments for the hippocampus (Kühn et al., 2020).

At the same time, living close to green spaces has been shown to be positively associated with brain health measures related to brain structure, such as cortical thickness, amygdala integrity, and to be negatively associated with brain atrophy (Besser et al., 2021; Crous-Bou et al., 2020; Kühn et al., 2017). A recent study reported that in individuals at risk for developing Alzheimer's dementia, large residential green areas are linked to higher cortical thickness in areas linked to Alzheimer's dementia, suggesting a possible role of nature in mitigating detrimental effects of urban environments on these brain regions (Crous-Bou et al., 2020). A study with older adults showed that living close to green space was associated with lower ventricular volume, which reflects global brain atrophy, again highlighting the potential positive link between green spaces and brain health (Besser et al., 2021). Furthermore, another study with older adults found a positive association between the coverage of urban green spaces in participants' neighbourhoods and the grey matter volume in the perigenual/subgenual anterior cingulate cortex (pACC/sACC), a region previously linked to depression. Conversely, the size of industrial and transportation areas was found to negatively correlate with the volume in these brain regions. Moreover, the presence of urban greenery accounted for additional variance compared industrial areas, suggesting that urban greenery may have an impact on brain structure beyond the detrimental effects of urban settings (Kühn et al., 2021). To understand the environmental factors contributing to brain plasticity in the elderly, Kühn and colleagues examined the association of forest coverage, urban green environment, water bodies, and wasteland with amygdala, pACC and dlPFC integrity (Kühn et al., 2017). They demonstrated a positive relationship between forest coverage in participants' neighbourhoods and amygdala integrity, suggesting that forests may have salutogenic effects on the health of the amygdala.

While these studies offer valuable insights, their cross-sectional design limits the ability to infer causality between environmental features and brain structure changes. It cannot be excluded that individuals with specific mental health characteristics or neurological traits might choose to live in greener surroundings.

1.5.2 Natural and urban environments and brain function

Beyond the relationship between an urban or natural environment and brain structure, several studies examined the relationship between these environments and brain function. Lederbogen and colleagues (2011) conducted a seminal study in which they investigated the relationship between urban and rural environments and brain function. Using functional magnetic resonance imaging (fMRI), they demonstrated that during a social stress task, activity in the amygdala, a brain region associated with stress (Inman et al., 2023; Roozendaal et al., 2009), was higher in urban compared to rural dwellers. Furthermore, the association between current city living and amygdala activity during a social stress task increased stepwise, from participants living in rural areas to those living in towns, and was the highest in city dwellers. Additionally, the authors examined the association between early-life urbanicity and brain activity during the social stress task and found that early-life urbanicity was positively related to activity in the pACC, a brain region that modulates amygdala activity and stress. This study indicates that living and being raised in an urban environment may negatively affect brain function, reflected in heightened stress-related brain activity during social stress task. While this psychiatric research has highlighted the negative impact of urban environments, these results can also be interpreted through the lens of environmental psychology, suggesting that these findings may reflect the protective effects of natural environments on the brain activity of individuals living in less urbanised areas.

Similarly, another study showed that during experiencing stimuli activating the dopaminergic system, urban residents exhibited altered activity and modulatory capability within the midbrain dopamine system (Krämer et al., 2017). Specifically, they showed heightened activation in areas like the amygdala, medial orbitofrontal cortex, and pACC compared to rural residents. The results suggest that chronic stress, common in urban environments, might induce a dysregulation of the dopamine system, which is also implicated in mental disorders such as depression and schizophrenia. Another recent study focused on participants' real-time emotional responses in urban green spaces (Tost et al., 2019). It sought to understand the correlation between the intensity of their emotional response in urban green spaces and brain function during a task that elicits negative emotions. The authors found that experiencing positive emotions in green spaces was associated with reduced activity in the brain regions that regulate emotions, the dlPFC and in the ventromedial prefrontal cortex (vmPFC). Given that reduced activity in the dlPFC and vmPFC is commonly observed in individuals at higher risk for depression and anxiety disorder (Opel et al., 2017), the findings of this study suggest that green spaces may serve as a protective factor by compensating for reduced regulatory prefrontal capacity (Tost et al., 2019).

The preceding cross-sectional studies indicate that growing up in or living near natural environments is positively associated with brain structural health metrics as well as with a reduction in stress-related brain function. However, it is important to note that the causal relationship between the environment and brain measures cannot be established based on this evidence. Hence, it remains unclear whether the environment influences brain outcomes, according to the breeder hypothesis, or if individuals with healthier lifestyles, potentially leading to better brain health, choose to reside near green spaces, while those with mental health issues choose to move to cities for improved healthcare access, as proposed by the drift hypothesis. To determine causality, intervention studies are needed where brain outcomes are assessed before and after the exposure to natural versus urban environments, thereby establishing a direct link between the environment and brain metrics (Bratman et al., 2019; Tost et al., 2015).

Several studies in laboratory settings focused on visual aspects of the physical environment, in which photos of a natural versus an urban environment were presented, while brain activity was measured using fMRI. Viewing rural scenery was related to activity of the ACC, involved in cognitive and emotional processing, as well as in regions like the globus pallidus, putamen, and the head of the caudate nucleus, linked to pleasant activities and positive emotions such as happiness (T.-H. Kim et al., 2010). Conversely, urban scenes were associated with heightened activity in the occipital cortex, involved in visual processing, the hippocampus and parahippocampus, linked to memory processing, and visual memory, as well as in the amygdala, linked to fear, danger, and stress. Another fMRI study found increased activity in areas associated with visual processing and attention (cuneus, right cingulate gyrus, left precuneus) when viewing natural versus urban images (Tang et al., 2017). It is important to point out, however, that these studies often had small sample sizes, warranting caution in interpreting the results. The interpretability of these findings is additionally constrained by the heightened risk of reverse inference (Poldrack, 2006). Namely, changes in specific brain regions during presentation of natural and urban stimuli do not necessarily imply the involvement of psychological processes related to those brain regions. To address this limitation, interventional approaches have been suggested as a viable solution (Roberts & Christopoulos, 2018).

Studies using electroencephalography (EEG) have indicated that viewing photographs and videos of nature scenes compared to urban scenes promoted alpha waves, associated with relaxation (Grassini et al., 2019, 2022). Unlike MRI equipment, EEG is portable and has therefore been used to examine brain activity in settings in situ, such as observing a natural space from an office window (Elsadek et al., 2020). This study also found an increase in alpha waves when viewing natural space to an urban space, corroborating the results by Grassini and colleagues (Grassini et al., 2019, 2022). Additionally, a study using portable EEG during a 20-minute walk in a natural versus an urban environment showed enhanced connectivity between EEG electrodes during the exposure to nature, potentially implying improved neural processing

(Chen et al., 2016). However, additional research is needed to understand the relationship between the physical environment and brainwave patterns during exposure to the environment in situ.

While MRI methodology offers higher spatial resolution and can measure activity in deeper brain structures compared to EEG, its immobility prevents real-time measurements in real-world environments. Thus, MRI can only be used to assess changes in brain activity before and after exposure to natural or urban settings. To our knowledge, MRI methodology examining causal effects between an exposure to nature and brain outcomes has been applied in only one study so far, to investigate neural correlates of rumination. Bratman and colleagues (2015) conducted an fMRI intervention study in which participants went to a 90-minute walk in an urban versus a natural environment. Self-reported rumination level and neural activation measured before and after the walk revealed a decrease in negative thoughts after the nature walk and decreased activation of the subgenual prefrontal cortex (sgPFC), related to self-focused behavioural withdrawal, linked to rumination in depressed and healthy individuals. The authors suggest that the decrease in rumination, linked to sgPFC activity, may be one of the neural mechanisms by which exposure to nature positively impacts mental health.

In summary, neuroscientific studies have repeatedly shown associations between natural and urban environments and both brain structure and brain function. Nevertheless, the intervention studies necessary to establish a causal relationship between the physical environment and brain function and structure are scarce. Furthermore, the impact of interindividual differences in the relationship between the physical environment and mental health and the brain remains unexplored. The following section will provide an overview of the literature on how natural and urban environments impact individuals differently based on factors such as gender and age.

1.6 Interindividual differences in responses to natural and urban environments

This section focuses on the role of interindividual differences in shaping responses to natural and urban environments. It examines how factors like sex and age may influence individual responses to these environments.

1.6.1 Sex differences in responses to natural and urban environments

Several studies have shown that women might profit more from salutogenic effects of nature compared to men (Fernández Núñez et al., 2022). For instance, it has been shown that a reduced risk for poor mental health was related to neighbourhood green space characteristics (e.g., spacious, serene). While this finding showed a trend in men, it was statistically significant only in women (Annerstedt et al., 2012). A similar pattern emerged in a study linking residential green space with stress levels (Bos et al., 2016). Furthermore, a study with data from more than 94 000 participants showed that green environments had a protective effect on depression, which was more pronounced in women (Sarkar et al., 2018). An intervention study in which participants were sitting in a natural or an urban environment for 20 minutes showed that the exposure to nature had a higher stress-relieving effect on women than on men (Beil & Hanes, 2013). Furthermore, greater benefits of green spaces for women are also reflected in physiological markers of stress. Thus, women living in neighbourhoods with more green areas showed lower cortisol levels, whereas this was not case for men (Roe et al., 2013). Additionally, research in children showed that girls tend to favor nature-related activities compared to boys and that green area coverage was positively linked with reduced stress-related disorders in girls (Engemann et al., 2019).

To our knowledge, only one study explored sex differences in the relationship between the physical environment and brain health so far. The study revealed a negative association between brain gray matter volume and growing up in an urban environment only in men, but not in women (Haddad et al., 2015). Specifically, the longer men spent their childhood years in a big city, the lower their gray matter volume was in the pACC, whereas this was not case for women. Given that functional and structural changes in the pACC have been linked to schizophrenia (Radua et al., 2012) and men raised in cities have a heightened risk for developing this mental disorder (Aleman et al., 2003), the authors suggest that this neural mechanism could be related with upbringing in a city, increasing the risk for developing schizophrenia in men brought up in an urban environment. The factors responsible for driving sex differences in responses to natural and urban environments are not yet clear, and research on their effects on the brain is limited. Therefore, sex differences in the effects of nature and urban environments on brain function are yet to be investigated. The subsequent section presents a review of the literature that focuses on another interindividual difference: age. It summarises research on how natural and urban environments affect children.

1.6.2 Effects of natural and urban environments on children

Numerous studies have confirmed the beneficial impact of nature on mental health in adults (Barnes et al., 2019; Corazon et al., 2019; Kotera et al., 2022). However, the evidence concerning effects of exposure to natural and urban environments on children is scarce. Recent research has started to fill this gap, revealing significant associations between nature exposure in childhood and various health outcomes. Thus, it has been shown that children who frequently interact with nature tend to exhibit increased physical activity and a reduced risk of obesity (Islam et al., 2020). Furthermore, more green space in neighbourhoods of children up to 2 years old has been linked to improved neurodevelopment in early childhood (Liao et al., 2019). Additionally, access to such green spaces up to the age of 10 years has been shown to be associated with a reduced risk of developing mental disorders later in life (Engemann et al., 2019). Conversely, housing density of urban environments was linked to increased physiological stress in 12-month-old infants, highlighting the potential stress-inducing effects of urban settings (Wass et al., 2021).

Interestingly, the exposure of expectant mothers to natural environments has been linked to a positive health outcome of infants even before birth. Thus, pregnant women living in areas with abundant green space exhibited lower cortisol concentration in the umbilical cord, suggesting a less stressful intrauterine environment (Boll et al., 2020). Additionally, maternal contact with nature during pregnancy has been shown to correlate with higher infant birth weights and a reduced risk of preterm births (Islam et al., 2020). Infants are affected by their physical environment both directly and indirectly through their primary caregivers. Stressed mothers often have higher cortisol levels in their breastmilk (Tekgündüz et al., 2023), which can negatively influence infant's temperament (Glynn et al., 2007; Grey et al., 2013; Nolvi et al., 2018). These findings suggest that environmental stress can be communicated to infants via breast milk cortisol, shaping their emotions.

In summary, some research suggests that women might derive greater benefits from nature's positive influence on mental health compared to men. However, this relationship has not been conclusively established and the underlying reasons remain unclear. Despite the limited research on the impact of natural and urban environments on children, existing studies indicate that children living near nature tend to have better health, whereas those who live in a highly urban environment show increased stress. Nonetheless, the existing literature on the potential positive effects of nature in infants is currently sparse, and underlying mechanisms remain unclear. Moreover, causality cannot be established due to the cross-sectional design of these studies. In the following chapter I will recapitulate the findings reported above, discuss the existing gaps in the literature, and define the research questions for this dissertation.

2 Research questions

In our rapidly urbanizing world, urban living is increasingly linked to a higher likelihood of developing mental disorders, while nature is consistently found to benefit mental health (Furuyashiki et al., 2019; Kotera et al., 2022; Lopes et al., 2020; Peen et al., 2010; Pignon et al., 2023). Research indicates that exposure to natural environments enhances mood and reduces stress, including its physiological markers (Antonelli et al., 2019; Barnes et al., 2019; Chang et al., 2019; Corazon et al., 2019; M. M. Hansen et al., 2017; Kondo et al., 2018; Kotera et al., 2022; McMahan & Estes, 2015; Oh et al., 2017). Nevertheless, the neural underpinnings of these effects are yet to be understood. Research has demonstrated a relationship between features of the physical environment, such as population density or residential greenery, and brain functional and structural health metrics (Besser et al., 2021; Crous-Bou et al., 2020; Krämer et al., 2017; Kühn et al., 2017, 2020, 2021; Lederbogen et al., 2011; Tost et al., 2019). For example, rural residents have been shown to exhibit reduced stress-related amygdala activity during social stress tasks compared to urban dwellers (Lederbogen et al., 2011), and adolescents raised in rural settings exhibited greater left hippocampal volume than their urban counterparts (Kühn et al., 2020). However, due to the cross-sectional nature of these studies, the directionality and causality of these relationships remains unclear.

In order to establish the causal relationship between the natural and urban environments and the brain, intervention studies are essential (Bratman et al., 2019; Tost et al., 2015). To identify specific brain regions activated by natural and urban settings, several studies have investigated brain activity while participants viewed photos of these environments (T.-H. Kim et al., 2010; Tang et al., 2017). Nevertheless, the ecological validity of these studies is questionable, as it is debatable whether viewing two-dimensional images can truly replicate the multi-sensory experience of presence in a real-life environment. Moreover, interpretability of these studies is limited due to an increased risk of reverse inference (Poldrack, 2006). Therefore, it has been suggested that interventional approaches may provide a solution to overcome these shortcomings (Roberts & Christopoulos, 2018). Previous EEG studies have attempted to investigate the neural effects of natural and urban environments in situ (Chen et al., 2016; Elsadek et al., 2020). However, it is important to note that EEG primarily captures cortical surface neural activity, which has limited spatial resolution and restricted capability for measuring activity in deeper brain structures, including the limbic system, associated with emotion processing. To assess deeper brain structures, MRI is commonly employed, but its immobility restricts real-time measurements in situ. Therefore, MRI can be utilised in intervention studies to measure brain activity before and after exposure to natural or urban settings.

To the best of our knowledge, only one study so far has employed an interventional method using an fMRI paradigm (Bratman et al., 2015). This study investigated the causal relationship between a walk in a natural versus an urban environment and brain function. The study found that both rumination and activity in the sgPFC, which is associated with rumination, decreased following the nature walk compared to the walk in an urban setting. This suggests that nature may positively impact mental health by reducing rumination-related brain activity. Nevertheless, it has been suggested that social stress, more prevalent in urban environments, may be an important factor contributing to development of mental disorders in cities (Lederbogen et al., 2013; Pignon et al., 2023). Conversely, ample empirical evidence shows that in situ exposure to nature, as opposed to urban settings, reduces subjective and physiological markers of stress (Kondo et al., 2018; Kotera et al., 2022; Lopes et al., 2020; Oh et al., 2017). However, the specific neural processes behind the impact of natural and urban environments on stress are not yet understood. Additionally, while there are indications that interindividual differences, such as sex, may have a role in the interplay between natural and urban environments and mental health (Annerstedt et al., 2012; Fernández Núñez et al., 2022; Roe et al., 2013; Sarkar et al., 2018), the role of these differences in stress-related brain function in response to these environments remains to be investigated.

Moreover, despite numerous studies linking environmental factors to brain structure (Besser et al., 2021; Crous-Bou et al., 2020; Kühn et al., 2017, 2021), our understanding of the causal relationship between the physical environment and brain structure remains limited. Notably, in examining the link between the physical environment and mental and brain health, psychiatric research has typically highlighted the detrimental aspects of urban environments (Haddad et al., 2015; Lederbogen et al., 2011), whereas environmental psychology has focused more on beneficial effects of natural environments (Bratman et al., 2015; Grassini et al., 2019, 2022; Kühn et al., 2017, 2021). Therefore, it remains uncertain whether the potential differential effects of natural and urban environments are driven by the negative aspects of urban settings or the positive influences of nature (Pignon et al., 2023; Tost et al., 2015).

Another important aspect often underexplored in studying effects of the physical environment and mental health is the lifespan. It is not yet clear which age groups would profit from short-term exposures to nature and when during their life span individuals start to be affected by natural and urban environments. Previous research indicates that natural environments correlate with positive health outcomes in children (Engemann et al., 2019; Liao et al., 2019). However, there is still a lack of research on the potential benefits of nature on infants, and the underlying processes remain unclear. Additionally, existing research on children, being cross-sectional, cannot establish causality between the physical environment and the outcomes. The impact of parents within the close social context of children, especially infants, should be considered when examining environmental effects on them. Finally, while previous research has primarily focused on the effects of predetermined routes in natural and urban settings on subjective and objective stress indicators (Gidlow, Jones, et al., 2016; Grazuleviciene et al., 2016; Triguero-Mas et al., 2017; Tyrväinen et al., 2014), the evidence about the effects of residential, everyday natural and urban settings are still not sufficiently explored.

Based on this theoretical background, this dissertation aims to answer the following research questions:

Research question 1: In what ways does exposure to natural versus urban environments affect stress-related brain function and hippocampal structure?

Research question 2: Do differential effects of these environments stem more from the positive impacts of nature or the negative influences of urban environments?

Research question 3: Do natural and urban environments have distinct effects on stress-related brain activity in men and women?

Research question 4: Can the effects of exposure to residential natural versus urban environments be detected in infants, and are these effects also reflected in stress indicators of their mothers?

The following section summarises four individual papers that aim to examine short-term effects of exposure to natural versus urban environments on stress indicators, and brain function and structure from several angles. In *Paper I* (Sudimac et al., 2022), we demonstrate short-term causal effects of a one-hour walk in a natural versus an urban environment on stress-related amygdala activity, which decreased after the walk in nature, and remains unchanged after the walk in the urban environment. In *Paper* II (Sudimac & Kühn, 2022), we examined sex differences and found that this effect was more prominent in a female subsample. In the third paper (Sudimac & Kühn, 2024), we observed a an increased volume in the subiculum, a hippocampal subfield, following a walk in nature, but not after a urban walk (though the interaction did not withstand Bonferroni correction). In the fourth paper (Sudimac et al., 2024), we investigated effects of a walk in natural versus urban residential environments on behavioural and physiological indicators of stress in mothers and their infants, observing no significant difference in outcomes between these environments. The original papers are in the appendix of this dissertation.

3 Overview of papers

3.1 Paper I

Sudimac, S., Sale, V., & Kühn, S. (2022). How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature. *Molecular Psychiatry*, 27(11), 4446–4452. https://doi.org/10.1038/s41380-022-01720-6

Objective: In *Paper I*, we aimed to understand the short-term effects of a one-hour exposure to natural versus urban environment on stress-related brain activity.

Theoretical background: Urban living is linked to a higher risk of mental disorders, such as anxiety and depression (Peen et al., 2010; Pignon et al., 2023; Purtle et al., 2019). Conversely, it has been demonstrated that natural environments can positively affect mental health (Barnes et al., 2019; Kondo et al., 2018; Oh et al., 2017). However, the neural underpinnings of these effects are not well understood. In a seminal study, urban residents displayed heightened amygdala activity during a social stress task compared to rural residents, suggesting potential adverse effects of city living on stress-related brain activity (Lederbogen et al., 2011). Nevertheless, since this study is cross-sectional, it lacks the capacity to establish a cause-and-effect relationship. To the best of our knowledge, only one study has examined causal relationship between the physical environment and brain function, demonstrating that exposure to nature reduced sgPFC activity, which is linked to rumination (Bratman et al., 2015). However, no study has yet examined the causal effects of exposure to natural and urban environments on activity in stress-related brain regions. To address this gap, we conducted an intervention study using fMRI to explore effects of a one-hour walk in a natural versus an urban environment on stress-related brain activity.

Main findings: We observed that amygdala activity significantly decreased after a walk in a nature, whereas it remained stable after a walk in an urban environment. This suggests that exposure to nature may beneficially affect stress-related brain regions, potentially serving as a preventive strategy against stress-related mental health issues like anxiety and depression. These findings contribute to the development of evidence-based policies for green prescriptions and urban planning that prioritise the integration of natural elements into cities, with the goal of improving mental and brain health.

3.2 Paper II

Sudimac, S., & Kühn, S. (2022). A one-hour walk in nature reduces amygdala activity in women, but not in men. *Frontiers in Psychology*, *13,* 1–13. https://doi.org/10.3389/fpsyg.2022.931905

Objective: *Paper II* aimed to explore the impact of sex on the changes in stress-related amygdala activity following a one-hour walk in a natural versus an urban environment.

Theoretical background: While substantial evidence indicates that nature positively influences mental health aspects such as mood and stress (Barnes et al., 2019; Kondo et al., 2018; Oh et al., 2017), the impact of individual differences (e.g., sex) has not been thoroughly studied. Previous research showed that the positive association between residential green spaces and mental health was more pronounced in women (Annerstedt et al., 2012; Bos et al., 2016; Sarkar et al., 2018), and found that only women showed lower cortisol levels in greener living environments (Roe et al., 2013). Furthermore, a 20 minutes of exposure to nature had more pronounced stress-relieving effects on women compared to men (Beil & Hanes, 2013). However, the neural mechanisms behind these sex-specific differences have not yet been explored. *Paper I* revealed that amygdala activity decreased after a one-hour walk in a natural environment but remained the same after an urban walk. Expanding on these findings, *Paper II* explores how this effect varies between women and men, to deepen the understanding of the role of sex in the observed effects of natural versus urban environments on stress-related brain activity.

Main findings: Our research revealed that a one-hour walk in a natural environment significantly reduced amygdala activity in women, but not in men. In contrast, walks in urban environments did not elicit this effect. These neural responses align with previous studies, suggesting that women might derive greater benefits from salutogenic effects of nature. To our knowledge, *Paper II* is the first to identify sex differences in the impact of natural versus urban environments on brain function. These findings underscore the importance of considering sex but also other interindividual differences when examining the effects of environmental factors on stress and brain function. They have implications for evidence-based urban design policies, emphasising the need to account for individual differences when planning green spaces in urban areas.

3.3 Paper III

Sudimac, S., & Kühn, S. (2024). *Can a nature walk change your brain? Investigating hippocampal brain plasticity after one hour in a forest.* PsyArXiv. https://doi.org/10.31234/osf.io/g64bq [Manuscript under revision]

Objective: In *Paper III* the aim was to explore the causal relationship between a one-hour exposure to a natural versus an urban environment and structural brain changes, specifically changes in hippocampal formation.

Theoretical background: Previous research has shown an association between the physical environment and brain structure such as cortical thickness or gray matter volume (Besser et al., 2021; Crous-Bou et al., 2020; Kühn et al., 2017, 2021). Adolescents who grew up in rural environments were reported to have a larger left hippocampal formation compared to those raised in cities (Kühn et al., 2020). Nevertheless, the effects of short-term exposure to natural and urban environments on brain structure have not yet been investigated. Even though it is assumed that brain structure is rather stable, previous studies have shown rapid change in brain structure, occurring after hours or only several minutes following an intervention (Månsson et al., 2020; Taubert et al., 2016; Tost et al., 2010). Given the plasticity of the hippocampus (Sagi et al., 2012) and its association with rural and urban upbringing (Kühn et al., 2020), we examined the effects of a one-hour walk on hippocampal structure in *Paper III.*

Main findings: The study found that participants who took a one-hour walk in nature showed an increase in subiculum volume, a hippocampal subfield involved in stress response inhibition, whereas no change was observed in participants who walked in an urban environment. In line with *Paper I*, these results suggest beneficial effects of exposure to nature as opposed to negative effects of urban environments. Additionally, the increase in subiculum volume was negatively associated with changes in rumination after the nature walk. It is important to note that the environment-by-time interaction did not persist after Bonferroni correction for multiple comparisons, necessitating cautious interpretation of these results as well as the need for further investigation. Nevertheless, we hold the results to be important, since this is, to the best of our knowledge, the first study to examine the causal effects of natural and urban environments on brain structure. These findings suggest that short-term exposure to nature can induce measurable changes in hippocampal structure, potentially offering mental health benefits.

3.4 Paper IV

Sudimac, S., Drewelies, J., De Weerth C.* & Kühn, S.* (2024). *Effects of a walk in a residential natural vs. urban environment on objective and subjective stress indicators in mothers and their infants.* PsyArXiv. https://doi.org/10.31234/osf.io/pz83m
[Manuscript under revision]

* These authors share last authorship.

Objective: *Paper IV* sought to assess the impact of a walk in residential natural versus urban environments on stress levels in mothers and their infants. This study focused on both subjective and physiological stress indicators, including maternal self-reported stress levels, salivary cortisol in mothers and infants, and cortisol levels in mothers' breast milk.

Theoretical background: Research indicates that exposure to natural settings positively affects both subjective and physiological stress markers (Antonelli et al., 2019; Kondo et al., 2018). However, these studies predominantly focus on adults, leaving a gap in understanding the response of young children and infants to natural and urban settings. Previous research indicates that greater green space in children's neighbourhoods is associated with enhanced neurodevelopmental and mental health (Engemann et al., 2019; Liao et al., 2019). Nevertheless, the causal effects of natural versus urban environments on children remain unclear due to the cross-sectional nature of existing studies. Furthermore, to the best of our knowledge, the impact of natural and urban environments on infants has not been investigated. Acknowledging the close social bond between infants and their parents, this study employs an intervention design to explore potential variations in stress levels in mothers and their infant during walks in natural versus urban environments. Moreover, since it has been indicated that cortisol levels in maternal breast milk can affect infant stress (Glynn et al., 2007; Grey et al., 2013; Nolvi et al., 2018), we also aimed to examine whether effects of natural and urban environments on mothers can be observed in their breastmilk. Additionally, to enhance the ecological validity of the results, we aimed to explore the effects of residential natural and urban environments that were familiar to the participants. This approach was intended to ensure that the findings were more representative of everyday experiences and environments typically encountered by the study participants. This study, therefore, examined the short-term effects of walking in residential natural versus urban environments on both subjective and physiological stress measures in mothers and their infants.

Main findings: The study found no significant differences between exposure to residential natural and urban environments in affecting subjective maternal stress and physiological stress indicators in mothers and their infants. A decrease in cortisol concentrations was observed in both mothers and infants after walks in both natural and urban environments, suggesting that walking itself may have decreased physiological indicators of stress. However, it is as well plausible that the decrease in cortisol concentrations reflects daily cortisol fluctuations. Furthermore, mothers reported decreased stress levels following walks in both environments, alongside increased feelings of pleasantness and calmness. Additional exploratory results revealed a continued decrease in maternal salivary cortisol concentrations at least until one hour upon arriving from the nature walk, a pattern not observed after the urban walk. This points to the stress-relieving effects of natural environments in mothers, potentially manifesting with some delay. These findings highlight the complex role of environmental exposure in stress modulation, informing urban design policies to enhance well-being of residents, especially mothers and young children.

4 General discussion

This dissertation explores the short-term effects of an exposure to natural versus urban environments on behavioural and physiological stress indicators, stress-related brain function, and hippocampal structure. I approached this question through a series of four papers. *Paper I* demonstrated that stress-related amygdala activity decreased after a one-hour walk in nature, whereas it remained unchanged after a walk in an urban environment. In *Paper II*, we examined subsamples of women and men and observed that amygdala activity decreased after a walk in nature exclusively in women, with no reduction found in men. In *Paper III*, we explored the effects of a one-hour walk in a natural versus an urban environment on the hippocampal formation. We observed an increase in the volume of the subiculum, a hippocampal subfield, following the walk in nature, whereas the subiculum volume remained stable after walking in an urban environmnet (though the interaction did not withstand the Bonferroni correction). In *Paper IV*, our investigation focused on the impact of walking in residential natural versus urban environments on mothers and their infants. We found no significant difference between these environments on behavioural and physiological indicators of stress in mothers and their infants.

In the sections that follow, I will provide a comprehensive summary of the key findings of this dissertation. Firstly, I will discuss how the findings of this thesis asnwer the posed research questions and address how they relate to the theoretical accounts. Secondly, I will explore potential implications of the evidence presented in this thesis for health and urban design policy-making. Finally, I will address the primary limitations of this research and suggest possible directions for future studies.

4.1 Discussion of research questions

This dissertation sought to investigate the short-term effects of exposure to natural versus urban environments on stress, stress-related brain function, and hippocampal structure, with a specific focus on the research questions presented in Chapter 2.

4.2.1 Effects on stress-related brain function and hippocampal structure

To explore the causal relationship between the physical environment and stress-related brain function and hippocampal structure, we performed an intervention study using MRI (*Papers I – III*). Since previous studies reported diminished stress-related amygdala activity in rural compared to urban dwellers (Lederbogen et al., 2011), and a larger left hippocampal formation in participants raised in rural environments (Kühn et al., 2020), we examined how exposure to natural versus urban environments affects stress-related brain function and hippocampal structure (Research question 1). In *Paper I*, we discovered that stress-related amygdala activity decreased after a walk in nature, whereas it remained unchanged after a walk in an urban environment. These findings imply that only one hour of exposure to nature can be beneficial for the amygdala, a stress-related brain region. No significant interaction between time and environment was detected in anterior cingulate cortex (ACC) and dlPFC activity, indicating that the amygdala could be the primary stress-related brain region affected by exposure to nature. Furthermore, participants reported greater attention restoration and higher enjoyment levels after walking in nature than in an urban environment, aligning with the ART and supporting the findings related to stress-related brain function. Additionally, we introduced an fMRI paradigm that enables the examination of short-term effects of exposure to natural and urban environments in situ on stress-related brain function. To the best of our knowledge, this is the first study to demonstrate the causal effects of exposure to the physical environment on a stress-related brain region. These results align more with the breeder hypothesis, which suggests that environmental features influence brain and mental health, rather than the drift hypothesis, which posits that individuals with specific neurological or health traits choose to live in certain environments. Nonetheless, further studies are needed to assess the long-term persistence of the beneficial effect of nature on amygdala activity.

Interestingly, the positive impact of nature exposure on amygdala activity was localised to the right amygdala, which is consistent with a prior study indicating that lower amygdala activity during social stress in rural dwellers, compared to urban dwellers, was predominantly driven by the right amygdala (Lederbogen et al., 2011). Notably, activity in the right amygdala has been shown to be heightened during the processing of negative emotions in patients with schizophrenia (Pankow et al., 2013). Furthermore, a meta-analysis demonstrated that social environmental stress, such as childhood trauma or early life stress was associated with activity in several brain regions, with activity in the right amygdala being the most robust finding across a range of populations (Mothersill & Donohoe, 2016). Considering the findings from *Paper I* alongside prior research, right amygdala activity may be associated with social stress, particularly prevalent in urban settings.

The higher incidence of mental disorders in urban areas (Peen et al., 2010; Pignon et al., 2023; Purtle et al., 2019) may be partly attributed to social stress factors, such as the loss of a social group upon moving to a city or social isolation (Lederbogen et al., 2013; Pignon et al., 2023). Given that social stress tends to be more pronounced in urban environments, it is possible that urban residents experiencing elevated social stress levels may demonstrate heightened amygdala hyperexcitability. In research on rodents, it has been demonstrated that chronic stress causes amygdala hyperexcitability and alters amygdala function and structure (Roozendaal et al., 2009; Rosenkranz et al., 2010). Conversely, human studies indicated that social stress, such as being adopted at older ages, can alter amygdala volume (Tottenham et al., 2010), while urban residents have been found to have higher amygdala activity during social stress tasks compared to rural inhabitants (Lederbogen et al., 2011). Furthermore, a certain type of social stress, long-lasting social isolation, has been associated with an increased risk of depression and anxiety (House, 2001) —mental health issues that are more prevalent in cities (Peen et al., 2010; Pignon et al., 2023; Purtle et al., 2019) and linked with amygdala hyperactivity (Sehlmeyer et al., 2011; Siegle et al., 2007; Yang et al., 2010). Additionally, a systematic review highlighted that social fragmentation, a form of social stress characterised by weakened connections between individuals and society, is linked to increased psychosis rates, even after adjusting for various socio-economic factors (Ku et al., 2021). Moreover, it was suggested that urban upbringing is a key environmental factor in schizophrenia development, a psychotic disorder which is linked to alterations in the amygdala (Lawrie et al., 2003; Wright et al., 2002). Therefore, the results in *Paper I* suggest that contact with nature and a resultant reduction in amygdala engagement may buffer the negative impact of the city such as social stress, and serve as a preventive measure against developing symptoms of a mental disorder. With the rapid growth of urbanisation, the influence of urban environments on mental health is set to become even more significant in the following years (Krabbendam, 2005). This underscores the vital importance of urban planning in the development of both present and future cities. It is essential to integrate accessible green spaces within urban areas to improve the mental well-being of residents, highlighting how urban design can actively contribute to public mental health.

Interestingly, the observation that a consistent pattern of amygdala activity was noted after exposure to the natural environment in both the Fearful Faces Task (FFT) and the Montreal Imaging Stress Task (MIST), as well as during the viewing of neutral faces in the FFT, suggests that a one-hour walk in nature might globally benefit amygdala activity. This may imply that the nature walk increased the amygdala's threshold for activation, regardless of the specific task or stimuli. Therefore, we speculate that this short-term effect may reveal the mechanism behind the long-term effects of the physical environment on stress-related brain regions. The decrease in amygdala activity after of short-term exposure to nature might offer a mechanism explaining diminished amygdala activity during stress found in rural dwellers (Lederbogen et al., 2011). These beneficial short-term effects of nature on the amygdala could contribute to maintaining higher structural integrity of the amygdala observed in older individuals who live in areas with high forest coverage (Kühn et al., 2017). It is plausible that repeated exposure to nature may positively impact the amygdala by raising its activation threshold, resulting in reduced activity during stress and improved amygdala integrity in those residing near natural settings. Furthermore, such repeated exposures could lessen amygdala hyperactivation, which has been associated with trait anxiety (Sehlmeyer et al., 2011) and depression (Siegle et al., 2007; Yang et al., 2010). This may explain why proximity to green spaces has been shown to correlate with a lower risk of depression (Cohen-Cline et al., 2015; Gascon et al., 2015; Sarkar et al., 2018). Therefore, frequent interactions with nature by potentially reducing amygdala hyperactivation, could serve as a protective factor against the development of depressive symptoms. Nevertheless, additional longitudinal research is required to investigate the effects of exposure to the physical environment on different timeframes, as well as to better understand the connection between short-term effects and long-term changes in the brain.

In *Paper III*, we investigated the effects of a one-hour walk in a natural versus an urban environment on potential structural changes in the hippocampus, a brain region known to be associated with the environment of upbringing (Kühn et al., 2020) and for its high plasticity (Sagi et al., 2012). We found that the volume of the subiculum, a subfield of the hippocampus, increased after the walk in nature, while remaining unchanged after the urban walk. This finding challenges the perception of brain structure as a stable trait; however, growing evidence suggests that alterations in brain structure can occur within a span of hours or minutes (Karch et al., 2019; Kühn et al., 2022; Månsson et al., 2020; Sagi et al., 2012; Taubert et al., 2016; Tost et al., 2010). The subiculum plays a role in memory and spatial orientation (Keresztes et al., 2022; O'Mara, 2005). It is also involved in suppressing the stress-related hypothalamic–pituitary–adrenal (HPA) axis (O'Mara, 2005) and controlling anxiety (Mcnaughton, 2006). Therefore, this finding indicates that exposure to nature positively impacts a brain region involved in inhibiting stress response, aligning with the results from *Paper I*. Nevertheless, it is important to note that the interaction between environment and time did not persist after Bonferroni correction for multiple comparisons, which calls for a cautious interpretation of the results. Additionally, the observed increase in subiculum volume following nature walks correlated with reduced self-reported rumination. This is consistent with previous research showing decreased subiculum volume in patients with major depressive disorder, a condition marked by chronic stress and rumination (Harel et al., 2016). Thus, the results from *Paper I* and *Paper III* suggest that a one-hour walk in a natural compared to an urban environment differentially affects stress-related brain function and structure in a hippocampal subfield, linked to HPA inhibition.

4.2.2 Beneficial effects of natural environments

It has been discussed whether the association between the physical environment and brain measures was driven by positive effects of nature or negative effects of cities (Pignon et al., 2023; Tost et al., 2015). However, the predominantly cross-sectional nature of previous studies (Besser et al., 2021; Crous-Bou et al., 2020; Krämer et al., 2017; Kühn et al., 2017, 2020; Lederbogen et al., 2011; Tost et al., 2019) has limited their ability to address this issue. Therefore, in our research, we sought to determine whether differential effects of natural versus urban settings in *Papers I* and *III* were driven by beneficial impacts of natural environments or the adverse influences of urban settings (Research question 2). In *Papers I* and *III* we found that the interaction between environment and time in stress-related brain function and hippocampal structure was driven by a change during the walk in nature, whereas no change was observed after a walk in an urban environment. The observation of short-term changes suggests that nature contributed to stress recovery, yet we observe no evidence to indicate that exposure to urban environments adversely affects stress-related brain function and hippocampal structure. This aligns with the previous intervention study (Bratman et al., 2015) that also noted decreased sgPFC activity following a nature walk and no change after an urban walk. This is also in line with a cross-sectional study that found a positive correlation between urban greenery and increased gray matter volume in the pACC/sACC, indicating that urban greenery can have a positive impact on brain structure, which goes beyond the negative effects of city living.

The findings in *Paper I* and *Paper III* indicate that nature's health-promoting elements, like greenery and birdsong, extend beyond the mere absence of adverse urban features like air pollution and traffic noise. This may imply that the lack of green spaces in cities, rather than their detrimental effects, might more directly relate to the observed mental health decline in urban areas. These results have an important implication for urban design policies, as they underline that the presence of green spaces in cities may be essential for brain health. It is important to acknowledge that participants in the study conducted for *Paper I* and *Paper III* lived in an urban environment, probably similar to the urban environment they were exposed to during the urban walk. Thus, this familiarity might explain why amygdala activity and subiculum volume remained stable in participants exposed to the urban environment. Therefore, while the results show that the exposure to an urban environment did not further increase amygdala activity or further decrease subiculum volume, we cannot rule out the possibility that these effects are influenced by the participants' familiarity with the urban environment.

Conversely, it is possible that the nature path's novelty might affect stress-related brain function and hippocampal structure. Ideally, this issue could be addressed by introducing a control condition in a setting that is neither natural nor urban; however, identifying such a setting presents a challenge. A possible option could be walking on a treadmill in a plain white room. However, this setup could appear artificial and monotonous, making it nor fully comparable to the natural and urban walk. Therefore, future research should examine the effects of an unfamiliar urban environment and more urbanised than participants' everyday surroundings (with more traffic lanes, fewer trees etc.). Furthermore, future studies should consider examining the effects of natural and urban environments on participants who live in less urbanised areas such as towns. These approaches would level the familiarity with both nature and urban routes, making the interventions (walks) in both settings more comparable. In conclusion, since the categories of natural and urban are subjective and differ across different environments, cultures and individuals, further research is needed. This research should assess the effects of natural and urban environments on individuals from varied backgrounds to discern whether the relationship between the physical environment and the brain is driven by the positive effects of nature, the negative effects of urban settings, or a combination of both.

4.2.3 Sex-related differences

Since the role of the interindividual differences in neural effects of the physical environment remains unclear, our research aimed to investigate sex differences in the impact of a one-hour walk on amygdala activity (Research question 3). In *Paper II*, we found that amygdala activity decreased following the nature walk specifically in the female participants, but not in the male subgroup. This suggests that the health-promoting effects of nature on stress-related brain activity may be more pronounced in women. These results are consistent with prior studies that found that green residential environments were linked to a lower risk of developing mental disorders primarily in women (Annerstedt et al., 2012; Sarkar et al., 2018), and that more residential green spaces correlated with lower cortisol levels, again only in women (Roe et al., 2013). This is further supported by a recent review suggesting that the beneficial effects of nature might be more significant in women (Fernández Núñez et al., 2022). However, it is important to note that these earlier studies are cross-sectional and, as such, cannot establish causal relationships. In *Paper II*, to the best of our knowledge, we report a seminal finding demonstrating interindividual differences in the causal relationship between the physical environment and brain function. This marks an important step forward in understanding how environmental factors affect brain activity differently across sexes.

The reason behind potentially more prominent salutogenic effects of nature in women is not clear. Previous findings proposed that one factor may be a stronger connection to nature among women compared to men (Dean et al., 2018; Rosa et al., 2023). Additionally, it ha sbeen reported that women demonstrate a greater inclination towards eco-friendly consumer behaviours, such as showing a positive intention to buy green products and purchasing them more frequently (Zhao et al., 2021). Additionally, it remains uncertain whether the interindividual differences reported in *Paper II* reflect sex or gender differences, that is, whether they are related to biological factors affecting neural activity or social factors, namely learned patterns such as learned perceptions of nature that vary between genders, or the interplay of biological and social factors. Thus, following this initial examination of sex differences in the impact of natural and urban environments on brain activity, further research is necessary to validate these findings and clarify the underlying causes of these disparities. Understanding the varied effects of natural and urban environments on different sexes and genders is essential for the effective integration of these insights into health-related and urban planning related policy-making.

4.2.4 Effects on stress mothers and their infants

An underexplored aspect in the research on the effects of the physical environment effects on mental health is its developmental aspect. Moreover, while most prior research focused on predefined routes in natural and urban environments, its influence on everyday mood and stress remains underinvestigated. Therefore, *Paper IV* examines the causal relationship between exposure to residential natural versus urban environments and both objective and subjective stress indicators in mothers and their infants (Research question 4).

Contrary to our expectations, no significant difference was found in stress indicators between natural and urban walks. Nevertheless, both maternal and infant cortisol levels decreased after the walk, suggesting that walking itself, irrespective of the environment, may have reduced cortisol. It cannot be excluded, however, that this decrease was simply a reflection of the natural diurnal fluctuations of cortisol. Our results support previous findings that also did not observe cortisol reduction after exposure to natural versus urban environments (Gidlow, Jones, et al., 2016; Tyrväinen et al., 2014; Veitch et al., 2022). Moreover, a systematic review (Kondo et al., 2018) indicates there is no conclusive evidence on urban green spaces in reducing cortisol levels. Notably, previous studies showing cortisol reduction often involved longer immersions in more remote forest environments (Antonelli et al., 2019), whereas in our study the exposure was shorter and took place in the participants' neighbourhoods. This suggests that longer exposure or more remote natural areas are necessary to provide a salutogenic effect of nature, or that the familiarity of an everyday residential environment may have diminished beneficial effects of nature. Furthermore, in *Paper I,* a walk in a remote natural setting showed a beneficial effect on amygdala activity, suggesting that exposure to distant natural areas with more natural features such as a forest may be key for stress relief.

The diversity of residential routes within natural and urban environments in *Paper IV* differs significantly from previous studies that often used more controlled paths. As a result, the extent to which an environment needs to consist of urban or natural features to influence subjective and objective stress indicators remains uncertain. In *Paper I*, we observed the effect of an urban forest outside the city on amygdala activity, but it is still unclear whether urban green spaces within a city can reduce objective stress markers.

Additional exploratory findings showed that in mothers cortisol concentrations continued to decrease until at least one hour following the walk in a natural environment, whereas such a decrease was not observed after the urban walk. This indicates that exposure to nature may have had stress relieving effects for mothers, but at a later timepoint. Nevertheless, additional research is required to replicate these results and to ascertain the duration of nature's potential beneficial effects on physiological indicators of stress.

Paper IV is also notable, as, to our knowledge, it is the first study to examine effects of exposure to natural versus urban environments in a holistic setting that include mothers and their infants. However, mothers' caregiving role may have impacted maternal stress levels during the walks and might have altered behavioural and physiological indicators of stress, potentially overshadowing the environmental effects. Additionally, the mothers' autonomous data collection might also have affected stress levels. On the other hand, the absence of the expected effect in infants may be attributed to very early age, therefore we recommend future research to examine whether short-term exposure to natural and urban environments affect children of older ages. Future research should consider these factors and extend investigations to other caregiver-child dyads, exploring optimal walk durations and frequencies of visiting nature for stress reduction.

4.2.5 Perspective on theoretical accounts

Objective measures of stress presented in all papers of this dissertation offer a new insight regarding the main theories in the field of environmental psychology, ART and SRT. In *Papers I* and *IV*, participants reported greater restoration of their attention following the walk in nature compared to the walk in an urban environment, which aligns with ART, focusing on cognition and positing that nature restores directed attention (Kaplan, 1995). Notably, within the ART framework, we examined potential changes in working memory capacity after the nature versus urban walk in *Papers I* and *IV*, but we observed no significant changes. However, it is important to note that in *Paper I*, the post-walk working memory test was conducted immediately after an MRI stress-inducing paradigm, not following the walks. In *Paper IV*, mothers reported distractions from their infants during the task, which could have affected the results. Therefore, these findings warrant careful interpretation and necessitate further research. On the other hand, SRT emphasises stress reduction, suggesting that exposure to nature inherently reduces stress in humans due to our evolutionary history, subsequently enhancing attention (Ulrich et al., 1991). While these theories are complementary frameworks (Berto, 2014; Joye & Van Den Berg, 2018), ART highlights the importance of improving cognition and SRT importance of reducing stress. Therefore, our research, particularly in *Paper I*, aligns more strongly with SRT. We observed a decrease in amygdala activity, a brain region involved in modulating stress response, without significant changes in areas associated with cognition (dlPFC and ACC).

Nevertheless, our findings are most congruent with the recently proposed NBRT (White et al. 2023). This theory proposes that contact with nature can create biopsychosocial resilience that helps in preventing or reducing stress. *Paper I* suggests that even short-term exposure to nature may build biological resilience, by strengthening the adaptive nervous system to stressors. Therefore, even a one-hour walk in nature may contribute to creating biological resilience related to the nervous system, reflected in diminished stress-related neural activity after the exposure to nature. According to NBRT, over time, this resilience may help counteract the effects of stressors, potentially resulting in lower amygdala activity during social stress observed in rural compared to urban dwellers (Lederbogen et al., 2011). Within this approach, diminished stress-related activity during social stress in rural dwellers would represent enhanced psychological and biological resilience to stressors due to frequents contact with nature in rural inhabitants. Additionally, NBRT underlies the importance of social context during the walk, such as sharing nature experience with others, what we tackled in *Paper IV*, as well as interindividual differences and age span, which were tackled in *Paper II* and *Paper IV*.

4.2 Potential application to health and urban design policies

This dissertation has important applications for health policies, such as green prescription, as well as urban design policies. The concept of a green prescription refers to a health professional's advice for a patient to engage in nature-based activities, such as walking in a park or gardening, as part of their treatment plan (Robinson & Breed, 2019; A. E. Van den

Berg, 2017). This approach is particularly focused on patients with mental health issues like depression, anxiety, and stress-related disorders (Adewuyi et al., 2023). *Paper I* suggests therapeutic benefits of natural environments on brain regions associated with stress and together with previous research contributes to evidence for nature-based activities in treatment plans, especially for conditions linked to stress. This study not only contributes to the scientific basis for green prescriptions but also encourages healthcare providers to consider nature-based strategies as part of a holistic approach to mental health care. While *Paper IV* does not conclusively demonstrate more beneficial effects of natural environments on stress compared to urban settings, it is important to note that participants went for a walk in residential areas. Future research should investigate whether more remote natural settings, such as the urban forests examined in *Paper I*, might offer greater benefits for nature-based treatments. This exploration is essential to discern the optimal types of natural environments for green prescriptions.

Another potential application of this research lies in shaping urban design policies. The positive effects of nature on mental health stress the importance of incorporating green spaces into urban landscapes to improve the quality of life for city residents (McCay et al., 2019; Olszewska-Guizzo, 2021). In this dissertation, *Papers I* and *III* emphasise the necessity of integrating natural elements into urban environments due to their salutogenic effects on brain health. The observed benefits underscore the urgency for urban designs that incorporate accessible green spaces, parks, and other natural features as fundamental elements of urban infrastructure. Additionally, the findings from *Paper IV* highlight the significance of designing walkable cities to facilitate stress reduction. Therefore, these insights collectively suggest that urban planning should not only focus on the functional aspects of city design, but also prioritise features that positively affect mental and brain health of its inhabitants.

4.3 Limitations and future directions

In this dissertation, we explored the effects of short-term exposure to natural versus urban environments on stress, stress-related brain function, and hippocampal structure. In this work, of course, there are certain limitations that should be discussed. The sample used in this dissertation predominantly consists of WEIRD (Western, Educated, Industrialised, Rich, and Democratic) individuals, which inherently limits the generalisability of our results. Moreover, as our participants lived in an urban environment, the generalisability of the results is limited to city dwellers. In *Papers I – III* it is also probable that the urban environment, being their everyday setting, was more familiar to them than the nature route. Therefore, as already mentioned, we cannot entirely rule out that observed effects on stress-related brain function and hippocampal structure might be partly attributed to the novelty of the natural environment. To account for previous familiarity with the environments and to broaden the applicability of these findings, future research should investigate the effects of exposure to natural versus urban environments among individuals living in towns and rural areas.

Importantly, the definitions of what constitutes a natural environment and an urban environment are not clearly established. In *Papers I – III* we characterised natural environment as “urban forest in a city of Berlin” and the urban environment as “a busy street in Berlin with shopping malls” (Sudimac et al., 2022). In *Paper IV* we focused on participants’ residential areas and defined the natural environment as “a nearby park that participants typically visit” and urban environment as “a nearby busy street with traffic that participants typically use for grocery shopping or similar activities” (Sudimac et al., 2024). However, it is important to point out that these definitions might not correspond to the concepts of natural and urban environments in other countries or cultures. Furthermore, these concepts may differ between inhabitants within the same city, influenced by different degrees of natural and built elements in their neighborhoods. Therefore, future research should document the environments used in studies with greater transparency and detail. This would provide a clearer understanding of the similarities and differences in natural and urban environments across various studies. Following the recommendations of Barnes and colleagues (2019), this approach would also support the evidence-based integration of natural environment features into urban design planning.

In *Papers I – III*, the specific natural elements responsible for the positive effects of nature on amygdala activity and hippocampal volume remain unidentified. While our aim was to examine a typical walk in natural and urban settings as a holistic experience, encompassing all different aspects between natural and urban environments, the specific natural features driving the effects of nature on the brain have yet to be determined. Thus, it is currently unclear whether the beneficial effects of nature on amygdala activity and hippocampal volume are due to greenery, birdsong, natural odours, their combination, or other factors. To address this, our next fMRI study, as outlined in the preregistration (Sudimac & Kühn, 2023), is designed to disentangle the effects of different natural features, by exploring changes in stress-related brain activity as an effect of various types of natural environments, such as forest, a waterscape, and a grassland. Identifying these active ingredients of nature would also contribute to integrate natural features into every day setting for individuals who, due to various reasons, cannot access outdoors natural environments. Another challenging yet important direction for examining specific natural features beneficial for mental and brain health would be to integrate MRI with VR technology. This innovative approach would allow for the manipulation of a variety of natural features within a realistic virtual setting, while simultaneously measuring their effects on brain activity. Integration of MRI methodology with VR presents an opportunity to systematically study specific aspects of natural environments and their impact on mental and brain health in a controlled yet immersive manner. Disentangling specific features of the natural environment that are salutogenic for mental and brain health is crucial for formulating evidence-based urban design policies. Such knowledge is key to developing urban spaces that are not only aesthetically pleasing but also restorative for mental health, underlining the importance of accessible green areas as a public health necessity.

An important yet unanswered question revolves not only around identifying the active ingredients in nature that drive stress relief but also discerning whether exposure to nature has a unique stress-relieving effect, different from other enjoyable stimuli. Previous research has shown that non-natural environments, such as museums and hospital rooms decorated as home environments can also induce restoration (Ohta et al., 2008; Packer & Bond, 2010). Furthermore, activities such as listening to classical music or meditating can also have stress-reducing effect (Chennafi et al., 2018; Marchand, 2012). Likewise, the results in *Paper IV* indicate that stress indicators were lower after the walk itself, irrespective of the environment. Therefore, future studies could investigate whether exposure to nature elicits more pronounced or distinct stress-relief effects compared to enjoyable activities or non-natural environments.

The rich diversity of natural environments worldwide, such as deserts, beaches, mountains, and forests, combined with distinct cultural views and values of nature, should be taken into consideration in future research. It should explore how interaction with these diverse natural settings, including distant nature or rural environments, affects the brain. An innovative approach could involve the use of mobile low-field MRI scanners (Aharoni et al., 2013) to examine how contact with distant nature or rural environments affects brain function and structure. Employing a portable MRI scanner would also enable the study of brain changes in response to nature in remote cultures, which attribute different meanings to nature than Western societies. Since MRI facilities are mostly in big cities, field research utilising mobile MRI can address some of the main limitations of this research, such as the focus on urban citizens, the examination of only city-based green spaces as representations of natural environments, and the inclusion of predominantly WEIRD samples. This diversity is crucial not only for a more comprehensive understanding of the impact of nature on mental health and brain function but also for the development and tailoring of medical and urban design policies to various cultural contexts.

An additional limitation to consider is that in *Papers I – III*, the collection of post-walk behavioural data occurred after participants had already undergone a stress-inducing MRI paradigm, rather than immediately following the walk. This design choice was driven by our primary focus on brain measures over behavioural outcomes. However, the data on mood and stress gathered post-walk primarily reflected participants' states while in the MRI scanner, rather than their states during the walk. This limitation hindered our ability to assess whether the walk in nature had an immediate effect on self-reported stress levels. For future research, we recommend administering short post-intervention questionnaires to evaluate mood and stress before collecting MRI data, which can itself be a source of stress. Such subjective data on mood and stress would enhance the understanding of the meaning of the observed neural activity. Additionally, during the walk, there may have been various factors beyond our control that could have affected the outcomes. Nevertheless, the random assignment of participants to the natural and urban conditions should have ensured an equal distribution of any confounding variables across both conditions.

In *Paper II*, a notable limitation was the restricted subsample size of men and women, which was insufficient for a three-way interaction analysis with participants' sex as an additional factor. Consequently, we recommend that future research examines this effect in a larger sample to determine whether there is an environment-by-time-by-sex interaction. A major limitation in *Paper III* was that the interaction effect did not persist after Bonferroni correction for multiple comparisons and, therefore, the findings should be considered exploratory. Nevertheless, we regard them as valuable since this was the first study to report changes in brain structure as an effect of short-term exposure to nature. We suggest that future studies revisit this effect with a larger sample size to validate our initial findings. In *Paper IV*, we aimed to explore the effects of residential natural and urban environments on mothers and their infants. However, the routes walked by participants may not be comparable due to wide variation in what constitutes urban and natural environments within a city. Future studies in this field might benefit from quantifying the effects of specific environmental features, such as forest coverage and air pollution, on stress levels, rather than relying on broad categories of natural and urban environments. Furthermore, it is unclear whether the reduced cortisol levels observed in mothers and infants after walks in both natural and urban environments are attributable to the walk itself or to cortisol's diurnal rhythm. Although the walks occurred in the afternoon, when cortisol levels are generally more stable (Å. M. Hansen et al., 2008), we cannot discount the possibility that the observed decrease in cortisol is part of the natural fluctuations of cortisol, which generally decreases throughout the day. Future research should consider several additional cortisol samplings before the walk and, ideally, on multiple non-experimental days at various times. This approach would establish a more accurate baseline, helping to ascertain whether the observed decrease in cortisol levels is influenced by the walk or simply reflects the usual daily fluctuations in cortisol levels in mothers and infants.

Additionally, as the mothers collected their own and their infants' saliva samples without an experimenter present, this could have additionally influenced their stress levels and hinder the effects of the environments on stress. While our approach in *Paper IV* aimed to enhance the ecological validity of the findings by exploring the impact of residential environments in participants' everyday settings, it also added complexity to the interpretation of the results. To overcome this limitation, in *Papers I – III*, participants followed a predefined route. However, undergoing an MRI paradigm in a lab with experimenters on site might question the naturalness of the study protocol and the ecological validity of the results. The controlled laboratory setting in *Papers I – III,* while advantageous for ensuring consistency in the study procedure among participants, may not entirely reflect real-world scenarios and their everyday experiences.

Another important constraint is a lack of understanding regarding the duration of nature's beneficial effects on stress-related neural activity and hippocampal structure. Additionally, the optimal length, exposure frequency, and the impact of individual differences and social context during exposure on these outcomes remain unclear. We addressed the duration of nature's effects in *Paper IV*, where we examined cortisol levels immediately after the walk, 30, and 60 minutes later. Nevertheless, additional measures are necessary to assess behavioural, physiological, and neural effects of exposure to natural versus urban environments over longer periods of time. Furthermore, the optimal duration of the walk remains unclear. In *Paper I*, we observed effects of a one-hour walk in nature on stress-related amygdala activity, however, it is not clear whether the effect would manifest after a shorter walk or persist, or even increase, following a longer walk. Prospective research should therefore investigate the impact of exposure to natural and urban environments of varying lengths, assessing whether shorter or longer durations have differential impact on stress-related responses.

An essential future direction is exploring long-term effects of spending time in nature. Longitudinal studies are necessary to understand the impacts of repeated exposure to nature over weeks or months. In *Papers II* and *IV*, we explored the effects of interindividual differences such as sex and age, as well as the social context during exposure. Nevertheless, future studies should focus on contrasting the effects of nature exposure across various age groups such as comparing young and older adults, and delve into the developmental trajectories of individuals to identify potential critical periods for exposure. In addition to addressing age differences, prospective research should expand its scope to encompass different sexes and genders. This broader approach can help identify those who may derive the greatest benefits from exposure to nature. Understanding the long-term effects of being in nature, the necessary duration and frequency of contact, as well as the influence of social context and individual differences, is essential for developing evidence-based green prescriptions. A crucial further step in this line of research would be examining the effects of exposure to natural and urban environments on psychiatric patients and individuals at risk for developing a mental disorder. Therefore, future studies should specifically examine which mental disorders or predisposing mental health challenges would be most positively impacted by exposure to nature. Furthermore, more longitudinal research involving clinical populations is necessary to firmly establish green prescriptions as valid clinical interventions (Kotera et al., 2022; Oh et al., 2017; A. E. Van den Berg, 2017). Continued research in this area will provide a more comprehensive understanding of the long-term effects and potential applications of nature-based therapies in clinical settings, thereby contributing to the evolving field of green prescriptions and nature-based health interventions.

4.4 Conclusion

In four publications, this cumulative dissertation explored the effects of a walk in natural versus urban environments on stress, stress-related brain function, and hippocampal structure. *Paper I* revealed that a one-hour walk in nature decreased stress-related amygdala activity, while it remained stable after a walk in an urban environment, suggesting salutogenic effects of short-term exposure to nature on brain regions related to stress. *Paper II* showed that the reduction in amygdala activity was observed in women, but not in men, emphasising the importance of examining interindividual differences in response to natural and urban environments, including sex disparities. *Paper III* investigated the effects of a one-hour walk a natural versus and urban environment on hippocampal structure. The volume of the subiculum, a hippocampal subfield associated with stress response inhibition, increased following the nature walk, while no changes were observed after the urban walk (though the interaction did not achieve statistical significance after applying the Bonferroni correction). This indicates that exposure to nature might have short-term impact on brain structure. *Paper IV* examined the effects of a walk in residential natural versus urban environments on behavioural and physiological indicators of stress in mothers and their infants. The study did not detect significant differences in subjective and physiological stress indicators between exposure to residential natural and urban environments in mothers and their infants. However, cortisol levels decreased in both mothers and infants after walks in both types of environments, possibly indicating the stress-reducing effects of walking itself or reflecting daily cortisol fluctuations.

In summary, this dissertation provides empirical insights into the causal effects of short-term exposure to natural versus urban environments on stress, stress-related brain function, and hippocampal structure. This research holds implications for health policies, including green prescription initiative, and urban design policies, emphasising the importance of integrating accessible green spaces into the urban environment for improved mental and brain health.

References

Adewuyi, F. A., Knobel, P., Gogna, P., & Dadvand, P. (2023). Health effects of green prescription: A systematic review of randomized controlled trials. *Environmental Research*, 1–15. https://doi.org/10.1016/j.envres.2023.116844

Aharoni, E., Vincent, G. M., Harenski, C. L., Calhoun, V. D., Sinnott-Armstrong, W., Gazzaniga, M. S., & Kiehl, K. A. (2013). Neuroprediction of future rearrest. *Proceedings of the National Academy of Sciences*, *110*(15), 6223–6228. https://doi.org/10.1073/pnas.1219302110

Alcock, I., White, M. P., Wheeler, B. W., Fleming, L. E., & Depledge, M. H. (2014). Longitudinal effects on mental health of moving to greener and less green urban areas. *Environmental Science & Technology*, *48*(2), 1247–1255. https://doi.org/10.1021/es403688w

Aleman, A., Kahn, R. S., & Selten, J.-P. (2003). Sex differences in the risk of schizophrenia: Evidence from meta-analysis. *Archives of General Psychiatry*, *60*(6), 565–571. https://doi.org/10.1001/archpsyc.60.6.565

Annerstedt, M., Östergren, P.-O., Björk, J., Grahn, P., Skärbäck, E., & Währborg, P. (2012). Green qualities in the neighbourhood and mental health: Results from a longitudinal cohort study in Southern Sweden. *BMC Public Health*, *12*, 1–13. https://doi.org/10.1186/1471-2458-12-337

Antonelli, M., Barbieri, G., & Donelli, D. (2019). Effects of forest bathing (shinrin-yoku) on levels of cortisol as a stress biomarker: A systematic review and meta-analysis. *International Journal of Biometeorology*, *63*(8), 1117–1134. https://doi.org/10.1007/s00484-019-01717-x

Barnes, M. R., Donahue, M. L., Keeler, B. L., Shorb, C. M., Mohtadi, T. Z., & Shelby, L. J. (2019). Characterizing nature and participant experience in studies of nature exposure for positive mental health: An integrative review. *Frontiers in Psychology*, *9*, 1–8. https://doi.org/10.3389/fpsyg.2018.02617

Beil, K., & Hanes, D. (2013). The influence of urban natural and built environments on physiological and psychological measures of stress—A pilot study. *International Journal of Environmental Research and Public Health*, *10*(4), 1250–1267. https://doi.org/10.3390/ijerph10041250

Benfield, J. A., Taff, B. D., Newman, P., & Smyth, J. (2014). Natural sound facilitates mood recovery. *Ecopsychology*, *6*(3), 183–188. https://doi.org/10.1089/eco.2014.0028

Berman, M. G., Kross, E., Krpan, K. M., Askren, M. K., Burson, A., Deldin, P. J., Kaplan, S., Sherdell, L., Gotlib, I. H., & Jonides, J. (2012). Interacting with nature improves cognition and affect for individuals with depression. *Journal of Affective Disorders*, *140*(3), 300–305. https://doi.org/10.1016/j.jad.2012.03.012

Berto, R. (2014). The role of nature in coping with psycho-physiological stress: A literature review on restorativeness. *Behavioral Sciences*, *4*(4), 394–409. https://doi.org/10.3390/bs4040394

Besser, L. M., Lovasi, G. S., Michael, Y. L., Garg, P., Hirsch, J. A., Siscovick, D., Hurvitz, P., Biggs, M. L., Galvin, J. E., Bartz, T. M., & Longstreth, W. T. (2021). Associations between neighborhood greenspace and brain imaging measures in non-demented older adults: The Cardiovascular health study. *Social Psychiatry and Psychiatric Epidemiology*, *56*(9), 1575–1585. https://doi.org/10.1007/s00127-020-02000-w

Besteher, B., Gaser, C., Spalthoff, R., & Nenadić, I. (2017). Associations between urban upbringing and cortical thickness and gyrification. *Journal of Psychiatric Research*, *95*, 114–120. https://doi.org/10.1016/j.jpsychires.2017.08.012

Bielinis, E., Takayama, N., Boiko, S., Omelan, A., & Bielinis, L. (2018). The effect of winter forest bathing on psychological relaxation of young Polish adults. *Urban Forestry & Urban Greening*, *29*, 276–283. https://doi.org/10.1016/j.ufug.2017.12.006

Boll, L. M., Khamirchi, R., Alonso, L., Llurba, E., Pozo, Ó. J., Miri, M., & Dadvand, P. (2020). Prenatal greenspace exposure and cord blood cortisol levels: A cross-sectional study in a middle-income country. *Environment International*, *144*, 1–11. https://doi.org/10.1016/j.envint.2020.106047

Bos, E., Van Der Meulen, L., Wichers, M., & Jeronimus, B. (2016). A primrose path? Moderating effects of age and gender in the association between green space and mental health. *International Journal of Environmental Research and Public Health*, *13*(5), 1–8. https://doi.org/10.3390/ijerph13050492

Bratman, G. N., Anderson, C. B., Berman, M. G., Cochran, B., De Vries, S., Flanders, J., Folke, C., Frumkin, H., Gross, J. J., Hartig, T., Kahn, P. H., Kuo, M., Lawler, J. J., Levin, P. S., Lindahl, T., Meyer-Lindenberg, A., Mitchell, R., Ouyang, Z., Roe, J., … Daily, G. C. (2019). Nature and mental health: An ecosystem service perspective. *Science Advances*, *5*(7), 1–14. https://doi.org/10.1126/sciadv.aax0903

Bratman, G. N., Hamilton, J. P., Hahn, K. S., Daily, G. C., & Gross, J. J. (2015). Nature experience reduces rumination and subgenual prefrontal cortex activation. *Proceedings of the National Academy of Sciences*, *112*(28), 8567–8572. https://doi.org/10.1073/pnas.1510459112

Brown, D. K., Barton, J. L., Pretty, J., & Gladwell, V. F. (2014). Walks4Work: Assessing the role of the natural environment in a workplace physical activity intervention. *Scandinavian Journal of Work, Environment & Health*, *40*(4), 390–399. https://doi.org/10.5271/sjweh.3421

Callaghan, A., McCombe, G., Harrold, A., McMeel, C., Mills, G., Moore-Cherry, N., & Cullen, W. (2021). The impact of green spaces on mental health in urban settings: A scoping review. *Journal of Mental Health*, *30*(2), 179–193. https://doi.org/10.1080/09638237.2020.1755027

Chang, Y., Ewert, A., Kamendulis, L. M., & Hocevar, B. A. (2019). Measuring biophysical and psychological stress levels following visitation to three locations with differing levels of nature. *Journal of Visualized Experiments*, *148*, 1–9. https://doi.org/10.3791/59272

Chen, Z., He, Y., & Yu, Y. (2016). Enhanced functional connectivity properties of human brains during in-situ nature experience. *PeerJ*, *4*, 1–25. https://doi.org/10.7717/peerj.2210

Chennafi, M., Khan, M. A., Li, G., Lian, Y., & Wang, G. (2018). Study of music effect on mental stress relief based on heart rate variability. In *2018 IEEE Asia Pacific Conference on Circuits and Systems (APCCAS)* (pp. 131–134). IEEE. https://ieeexplore.ieee.org/document/8605674/

Coensel, B. D., Vanwetswinkel, S., & Botteldooren, D. (2011). Effects of natural sounds on the perception of road traffic noise. *The Journal of the Acoustical Society of America*, *129*(4), EL148–EL153. https://doi.org/10.1121/1.3567073

Cohen-Cline, H., Turkheimer, E., & Duncan, G. E. (2015). Access to green space, physical activity and mental health: A twin study. *Journal of Epidemiology and Community Health*, *69*(6), 523–529. https://doi.org/10.1136/jech-2014-204667

Corazon, S. S., Sidenius, U., Poulsen, D. V., Gramkow, M. C., & Stigsdotter, U. K. (2019). Psycho-physiological stress recovery in outdoor nature-based interventions: A systematic review of the past eight years of research. *International Journal of Environmental Research and Public Health*, *16*(10), 1–21. https://doi.org/10.3390/ijerph16101711

Crous-Bou, M., Gascon, M., Gispert, J. D., Cirach, M., Sánchez-Benavides, G., Falcon, C., Arenaza-Urquijo, E. M., Gotsens, X., Fauria, K., Sunyer, J., Nieuwenhuijsen, M. J., & Luis Molinuevo, J. (2020). Impact of urban environmental exposures on cognitive performance and brain structure of healthy individuals at risk for Alzheimer's dementia. *Environment International*, *138*, 1–10. https://doi.org/10.1016/j.envint.2020.105546

Dean, J., Shanahan, D., Bush, R., Gaston, K., Lin, B., Barber, E., Franco, L., & Fuller, R. (2018). Is nature relatedness associated with better mental and physical health? *International Journal of Environmental Research and Public Health*, *15*(7), 1–18. https://doi.org/10.3390/ijerph15071371

Dye, C. (2008). Health and urban living. *Science*, *319*(5864), 766–769. https://doi.org/10.1126/science.1150198

Egner, L. E., Sütterlin, S., & Calogiuri, G. (2020). Proposing a framework for the restorative effects of nature through conditioning: Conditioned restoration theory. *International Journal of Environmental Research and Public Health*, *17*(18), 1–18. https://doi.org/10.3390/ijerph17186792

Elsadek, M., Liu, B., & Xie, J. (2020). Window view and relaxation: Viewing green space from a high-rise estate improves urban dwellers' wellbeing. *Urban Forestry & Urban Greening*, *55*, 1–8. https://doi.org/10.1016/j.ufug.2020.126846

Engemann, K., Pedersen, C. B., Arge, L., Tsirogiannis, C., Mortensen, P. B., & Svenning, J.-C. (2019). Residential green space in childhood is associated with lower risk of psychiatric disorders from adolescence into adulthood. *Proceedings of the National Academy of Sciences*, *116*(11), 5188–5193. https://doi.org/10.1073/pnas.1807504116

Ewert, A., & Chang, Y. (2018). Levels of nature and stress response. *Behavioral Sciences*, *8*(5), 1–13. https://doi.org/10.3390/bs8050049

Fernández Núñez, M.-B., Campos Suzman, L., Maneja, R., Bach, A., Marquet, O., Anguelovski, I., & Knobel, P. (2022). The differences by sex and gender in the relationship between urban greenness and cardiometabolic health: A systematic review. *Journal of Urban Health*, *99*(6), 1054–1067. https://doi.org/10.1007/s11524-022-00685-9

Furuyashiki, A., Tabuchi, K., Norikoshi, K., Kobayashi, T., & Oriyama, S. (2019). A comparative study of the physiological and psychological effects of forest bathing (Shinrin-yoku) on working age people with and without depressive tendencies. *Environmental Health and Preventive Medicine*, *24*(1), 1–11. https://doi.org/10.1186/s12199-019-0800-1

Garrett, J. K., Clitherow, T. J., White, M. P., Wheeler, B. W., & Fleming, L. E. (2019). Coastal proximity and mental health among urban adults in England: The moderating effect of household income. *Health & Place*, *59*, 1–11. https://doi.org/10.1016/j.healthplace.2019.102200

Gascon, M., Triguero-Mas, M., Martínez, D., Dadvand, P., Forns, J., Plasència, A., & Nieuwenhuijsen, M. (2015). Mental health benefits of long-term exposure to residential green and blue spaces: A systematic review. *International Journal of Environmental Research and Public Health*, *12*(4), 4354–4379. https://doi.org/10.3390/ijerph120404354

Geary, R. S., Thompson, D., Mizen, A., Akbari, A., Garrett, J. K., Rowney, F. M., Watkins, A., Lyons, R. A., Stratton, G., Lovell, R., Nieuwenhuijsen, M., Parker, S. C., Song, J., Tsimpida, D., White, J., White, M. P., Williams, S., Wheeler, B. W., Fry, R., & Rodgers, S. E. (2023). Ambient greenness, access to local green spaces, and subsequent mental health: A 10-year longitudinal dynamic panel study of 2·3 million adults in Wales. *The Lancet Planetary Health*, *7*(10), 809–818. https://doi.org/10.1016/S2542-5196(23)00212-7

Gidlow, C. J., Jones, M. V., Hurst, G., Masterson, D., Clark-Carter, D., Tarvainen, M. P., Smith, G., & Nieuwenhuijsen, M. (2016). Where to put your best foot forward: Psycho-physiological responses to walking in natural and urban environments. *Journal of Environmental Psychology*, *45*, 22–29.

Gidlow, C. J., Randall, J., Gillman, J., Smith, G. R., & Jones, M. V. (2016). Natural environments and chronic stress measured by hair cortisol. *Landscape and Urban Planning*, *148*, 61–67. https://doi.org/10.1016/j.landurbplan.2015.12.009

Glaeser, E. (2011). *Triumph of the city: How urban spaces make us human*. Pan Macmillan.

Glynn, L. M., Davis, E. P., Schetter, C. D., Chicz-DeMet, A., Hobel, C. J., & Sandman, C. A. (2007). Postnatal maternal cortisol levels predict temperament in healthy breastfed infants. *Early Human Development*, *83*(10), 675–681. https://doi.org/10.1016/j.earlhumdev.2007.01.003

Grassini, S., Revonsuo, A., Castellotti, S., Petrizzo, I., Benedetti, V., & Koivisto, M. (2019). Processing of natural scenery is associated with lower attentional and cognitive load compared with urban ones. *Journal of Environmental Psychology*, *62*, 1–11. https://doi.org/10.1016/j.jenvp.2019.01.007

Grassini, S., Segurini, G. V., & Koivisto, M. (2022). Watching nature videos promotes physiological restoration: Evidence from the modulation of alpha waves in electroencephalography. *Frontiers in Psychology*, *13*, 1–14. https://doi.org/10.3389/fpsyg.2022.871143

Grazuleviciene, R., Vencloviene, J., Kubilius, R., Grizas, V., Danileviciute, A., Dedele, A., Andrusaityte, S., Vitkauskiene, A., Steponaviciute, R., & Nieuwenhuijsen, M. (2016). Tracking restoration of park and urban street settings in coronary artery disease patients. *International Journal of Environmental Research and Public Health*, *13*(6), 1–9. https://doi.org/10.3390/ijerph13060550

Grey, K. R., Davis, E. P., Sandman, C. A., & Glynn, L. M. (2013). Human milk cortisol is associated with infant temperament. *Psychoneuroendocrinology*, *38*(7), 1178–1185. https://doi.org/10.1016/j.psyneuen.2012.11.002

Gruebner, O., Rapp, M. A., Adli, M., Kluge, U., Galea, S., & Heinz, A. (2017). Cities and mental health. *Deutsches Ärzteblatt International*, 1–9. https://doi.org/10.3238/arztebl.2017.0121

Haddad, L., Schafer, A., Streit, F., Lederbogen, F., Grimm, O., Wust, S., Deuschle, M., Kirsch, P., Tost, H., & Meyer-Lindenberg, A. (2015). Brain structure correlates of urban upbringing, an environmental risk factor for schizophrenia. *Schizophrenia Bulletin*, *41*(1), 115–122. https://doi.org/10.1093/schbul/sbu072

Hansen, Å. M., Garde, A. H., & Persson, R. (2008). Sources of biological and methodological variation in salivary cortisol and their impact on measurement among healthy adults: A review. *Scandinavian Journal of Clinical and Laboratory Investigation*, *68*(6), 448–458. https://doi.org/10.1080/00365510701819127

Hansen, M. M., Jones, R., & Tocchini, K. (2017). Shinrin-yoku (forest bathing) and nature therapy: A state-of-the-art review. *International Journal of Environmental Research and Public Health*, *14*(8), 1–48. https://doi.org/10.3390/ijerph14080851

Harel, E. V., Tennyson, R. L., Fava, M., & Bar, M. (2016). Linking major depression and the neural substrates of associative processing. *Cognitive, Affective, & Behavioral Neuroscience*, *16*(6), 1017–1026. https://doi.org/10.3758/s13415-016-0449-9

Harriss, L., & Hawton, K. (2011). Deliberate self-harm in rural and urban regions: A comparative study of prevalence and patient characteristics. *Social Science & Medicine*, *73*(2), 274–281.

Hedblom, M., Gunnarsson, B., Iravani, B., Knez, I., Schaefer, M., Thorsson, P., & Lundström, J. N. (2019). Reduction of physiological stress by urban green space in a multisensory virtual experiment. *Scientific Reports*, *9*(1), 1–11. https://doi.org/10.1038/s41598-019-46099-7

House, J. S. (2001). Social isolation kills, but how and why? *Psychosomatic Medicine*, *63*(2), 273–274. https://doi.org/10.1097/00006842-200103000-00011

Inman, C. S., Hollearn, M. K., Augustin, L., Campbell, J. M., Olson, K. L., & Wahlstrom, K. L. (2023). Discovering how the amygdala shapes human behavior: From lesion studies to neuromodulation. *Neuron*, *111*(24), 3906–3910. https://doi.org/10.1016/j.neuron.2023.09.040

Islam, M. Z., Johnston, J., & Sly, P. D. (2020). Green space and early childhood development: A systematic review. *Reviews on Environmental Health*, *35*(2), 189–200. https://doi.org/10.1515/reveh-2019-0046

Joye, Y., & Van Den Berg, A. E. (2018). Restorative Environments. In L. Steg & J. I. M. Groot (Eds.), *Environmental Psychology* (1st ed., pp. 65–75). Wiley. https://doi.org/10.1002/9781119241072.ch7

Kaplan, S. (1995). The restorative benefits of nature: Toward an integrative framework. *Journal of Environmental Psychology*, *15*(3), 169–182. https://doi.org/10.1016/0272-4944(95)90001-2

Karch, J. D., Filevich, E., Wenger, E., Lisofsky, N., Becker, M., Butler, O., Mårtensson, J., Lindenberger, U., Brandmaier, A. M., & Kühn, S. (2019). Identifying predictors of within-person variance in MRI-based brain volume estimates. *NeuroImage*, *200*, 575–589. https://doi.org/10.1016/j.neuroimage.2019.05.030

Keresztes, A., Raffington, L., Bender, A. R., Bögl, K., Heim, C., & Shing, Y. L. (2022). Longitudinal developmental trajectories do not follow cross-sectional age associations in hippocampal subfield and memory development. *Developmental Cognitive Neuroscience*, *54*, 101085. https://doi.org/10.1016/j.dcn.2022.101085

Kim, S. N., Kang, D.-H., Yun, J.-Y., Lee, T. Y., Jung, W. H., Jang, J. H., & Kwon, J. S. (2013). Impact of the BDNF Val66Met polymorphism on regional brain gray matter volumes: Relevance to the stress response. *Psychiatry Investigation*, *10*(2), 1–7. https://doi.org/10.4306/pi.2013.10.2.173

Kim, T.-H., Jeong, G.-W., Baek, H.-S., Kim, G.-W., Sundaram, T., Kang, H.-K., Lee, S.-W., Kim, H.-J., & Song, J.-K. (2010). Human brain activation in response to visual stimulation with rural and urban scenery pictures: A functional magnetic resonance imaging study. *Science of The Total Environment*, *408*(12), 2600–2607. https://doi.org/10.1016/j.scitotenv.2010.02.025

Kobayashi, H., Park, B.-J., & Miyazaki, Y. (2012). Normative references of heart rate variability and salivary alpha-amylase in a healthy young male population. *Journal of Physiological Anthropology*, *31*(1), 1–8. https://doi.org/10.1186/1880-6805-31-9

Kobayashi, H., Song, C., Ikei, H., Park, B.-J., Kagawa, T., & Miyazaki, Y. (2019). Combined effect of walking and forest environment on salivary cortisol concentration. *Frontiers in Public Health*, *7*, 1–6. https://doi.org/10.3389/fpubh.2019.00376

Kondo, M., Fluehr, J., McKeon, T., & Branas, C. (2018). Urban green space and its impact on human health. *International Journal of Environmental Research and Public Health*, *15*(3), 1–28. https://doi.org/10.3390/ijerph15030445

Kotera, Y., Richardson, M., & Sheffield, D. (2022). Effects of shinrin-yoku (forest bathing) and nature therapy on mental health: A systematic review and meta-analysis. *International Journal of Mental Health and Addiction*, *20*(1), 337–361. https://doi.org/10.1007/s11469-020-00363-4

Krabbendam, L. (2005). Schizophrenia and urbanicity: A major environmental influence–Conditional on genetic risk. *Schizophrenia Bulletin*, *31*(4), 795–799. https://doi.org/10.1093/schbul/sbi060

Krabbendam, L., Van Vugt, M., Conus, P., Söderström, O., Abrahamyan Empson, L., Van Os, J., & Fett, A.-K. J. (2021). Understanding urbanicity: How interdisciplinary methods help to unravel the effects of the city on mental health. *Psychological Medicine*, *51*(7), 1099–1110. https://doi.org/10.1017/S0033291720000355

Krämer, B., Diekhof, E. K., & Gruber, O. (2017). Effects of city living on the mesolimbic reward system—An fMRI study. *Human Brain Mapping*, 1–10. https://doi.org/10.1002/hbm.23600

Ku, B. S., Compton, M. T., Walker, E. F., & Druss, B. G. (2021). Social fragmentation and schizophrenia: A systematic review. *The Journal of Clinical Psychiatry*, *83*(1), 38587. https://doi.org/10.4088/JCP.21r13941

Kühn, S., Banaschewski, T., Bokde, A. L. W., Büchel, C., Quinlan, E. B., Desrivières, S., Flor, H., Grigis, A., Garavan, H., Gowland, P., Heinz, A., Ittermann, B., Martinot, J.-L., Martinot, M. L. P., Nees, F., Orfanos, D. P., Paus, T., Poustka, L., Millenet, S., … Gallinat, J. (2020). Brain structure and habitat: Do the brains of our children tell us where they have been brought up? *NeuroImage*, *222*, 1–7. https://doi.org/10.1016/j.neuroimage.2020.117225

Kühn, S., Düzel, S., Eibich, P., Krekel, C., Wüstemann, H., Kolbe, J., Martensson, J., Goebel, J., Gallinat, J., Wagner, G. G., & Lindenberger, U. (2017). In search of features that constitute an “enriched environment” in humans: Associations between geographical properties and brain structure. *Scientific Reports*, *7*(1), 11920. https://doi.org/10.1038/s41598-017-12046-7

Kühn, S., Düzel, S., Mascherek, A., Eibich, P., Krekel, C., Kolbe, J., Goebel, J., Gallinat, J., Wagner, G. G., & Lindenberger, U. (2021). Urban green is more than the absence of city: Structural and functional neural basis of urbanicity and green space in the neighbourhood of older adults. *Landscape and Urban Planning*, *214*, 1–8. https://doi.org/10.1016/j.landurbplan.2021.104196

Kühn, S., Mascherek, A., Filevich, E., Lisofsky, N., Becker, M., Butler, O., Lochstet, M., Mårtensson, J., Wenger, E., Lindenberger, U., & Gallinat, J. (2022). Spend time outdoors for your brain – an in-depth longitudinal MRI study. *The World Journal of*

Biological Psychiatry, *23*(3), 201–207. https://doi.org/10.1080/15622975.2021.1938670

Lammeyer, S., Dietsche, B., Dannlowski, U., Kircher, T., & Krug, A. (2019). Evidence of brain network aberration in healthy subjects with urban upbringing – A multimodal DTI and VBM study. *Schizophrenia Research*, *208*, 133–137. https://doi.org/10.1016/j.schres.2019.03.027

Lawrie, S. M., Whalley, H. C., Job, D. E., & Johnstone, E. C. (2003). Structural and functional abnormalities of the amygdala in schizophrenia. *Annals of the New York Academy of Sciences*, *985*(1), 445–460. https://doi.org/10.1111/j.1749-6632.2003.tb07099.x

Lederbogen, F., Haddad, L., & Meyer-Lindenberg, A. (2013). Urban social stress – Risk factor for mental disorders. The case of schizophrenia. *Environmental Pollution*, *183*, 2–6. https://doi.org/10.1016/j.envpol.2013.05.046

Lederbogen, F., Kirsch, P., Haddad, L., Streit, F., Tost, H., Schuch, P., Wüst, S., Pruessner, J. C., Rietschel, M., Deuschle, M., & Meyer-Lindenberg, A. (2011). City living and urban upbringing affect neural social stress processing in humans. *Nature*, *474*(7352), 498–501. https://doi.org/10.1038/nature10190

Lee, J. (2017). Experimental study on the health benefits of garden landscape. *International Journal of Environmental Research and Public Health*, *14*(7), 1–11. https://doi.org/10.3390/ijerph14070829

Lee, J., Tsunetsugu, Y., Takayama, N., Park, B.-J., Li, Q., Song, C., Komatsu, M., Ikei, H., Tyrväinen, L., Kagawa, T., & Miyazaki, Y. (2014). Influence of forest therapy on cardiovascular relaxation in young adults. *Evidence-Based Complementary and Alternative Medicine*, *2014*, 1–7. https://doi.org/10.1155/2014/834360

Li, H., Zhang, X., Wang, H., Yang, Z., Liu, H., Cao, Y., & Zhang, G. (2021). Access to nature via virtual reality: A mini-review. *Frontiers in Psychology*, *12*, 1–7. https://doi.org/10.3389/fpsyg.2021.725288

Li, Q., Morimoto, K., Nakadai, A., Inagaki, H., Katsumata, M., Shimizu, T., Hirata, Y., Hirata, K., Suzuki, H., Miyazaki, Y., Kagawa, T., Koyama, Y., Ohira, T., Takayama, N., Krensky, A. M., & Kawada, T. (2007). Forest bathing enhances human natural killer activity and expression of anti-cancer proteins. *International Journal of Immunopathology and Pharmacology*, *20*(2_suppl), 3–8. https://doi.org/10.1177/03946320070200S202

Liao, J., Zhang, B., Xia, W., Cao, Z., Zhang, Y., Liang, S., Hu, K., Xu, S., & Li, Y. (2019). Residential exposure to green space and early childhood neurodevelopment. *Environment International*, *128*, 70–76. https://doi.org/10.1016/j.envint.2019.03.070

Liu, F., Xu, J., Guo, L., Qin, W., Liang, M., Schumann, G., & Yu, C. (2023). Environmental neuroscience linking exposome to brain structure and function underlying cognition and behavior. *Molecular Psychiatry*, *28*(1), 17–27. https://doi.org/10.1038/s41380-022-01669-6

Lopes, S., Lima, M., & Silva, K. (2020). Nature can get it out of your mind: The rumination reducing effects of contact with nature and the mediating role of awe and mood. *Journal of Environmental Psychology*, *71*, 1–7. https://doi.org/10.1016/j.jenvp.2020.101489

Månsson, K. N., Cortes, D. S., Manzouri, A., Li, T.-Q., Hau, S., & Fischer, H. (2020). Viewing pictures triggers rapid morphological enlargement in the human visual cortex. *Cerebral Cortex*, *30*(3), 851–857. https://doi.org/10.1093/cercor/bhz131

Mao, G. X., Lan, X. G., Cao, Y. B., Chen, Z. M., He, Z. H., Lv, Y. D., Wang, Y. Z., Hu, X. L., Wang, G. F., & Jing, Y. (2012). Effects of short-term forest bathing on human health in a broad-leaved evergreen forest in Zhejiang Province, China. *Biomedical and*

Environmental Sciences, *25*(3), 317–324. https://doi.org/10.3967/0895-3988.2012.03.010

Mao, G.-X., Cao, Y.-B., Lan, X.-G., He, Z.-H., Chen, Z.-M., Wang, Y.-Z., Hu, X.-L., Lv, Y.-D., Wang, G.-F., & Yan, J. (2012). Therapeutic effect of forest bathing on human hypertension in the elderly. *Journal of Cardiology*, *60*(6), 495–502. https://doi.org/10.1016/j.jjcc.2012.08.003

Marchand, W. R. (2012). Mindfulness-based stress reduction, mindfulness-based cognitive therapy, and Zen meditation for depression, anxiety, pain, and psychological distress. *Journal of Psychiatric Practice®*, *18*(4), 233–252. https://doi.org/10.1097/01.pra.0000416014.53215.86

McCay, L., Bremer, I., Endale, T., Jannati, M., & Yi, J. (2019). Urban design and mental health. *Urban Mental Health*, 32. https://doi.org/10.1007/978-981-10-0752-1_12-1

McMahan, E. A., & Estes, D. (2015). The effect of contact with natural environments on positive and negative affect: A meta-analysis. *The Journal of Positive Psychology*, *10*(6), 507–519. https://doi.org/10.1080/17439760.2014.994224

Mcnaughton, N. (2006). The role of the subiculum within the behavioural inhibition system. *Behavioural Brain Research*, *174*(2), 232–250. https://doi.org/10.1016/j.bbr.2006.05.037

Mostajeran, F., Fischer, M., Steinicke, F., & Kühn, S. (2023). Effects of exposure to immersive computer-generated virtual nature and control environments on affect and cognition. *Scientific Reports*, *13*(1), 1–13. https://doi.org/10.1038/s41598-022-26750-6

Mothersill, O., & Donohoe, G. (2016). Neural effects of social environmental stress – an activation likelihood estimation meta-analysis. *Psychological Medicine*, *46*(10), 2015–2023. https://doi.org/10.1017/S0033291716000477

Nolvi, S., Uusitupa, H., Bridgett, D. J., Pesonen, H., Aatsinki, A., Kataja, E., Korja, R., Karlsson, H., & Karlsson, L. (2018). Human milk cortisol concentration predicts experimentally induced infant fear reactivity: Moderation by infant sex. *Developmental Science*, *21*(4), 1–8. https://doi.org/10.1111/desc.12625

Ochiai, H., Ikei, H., Song, C., Kobayashi, M., Miura, T., Kagawa, T., Li, Q., Kumeda, S., Imai, M., & Miyazaki, Y. (2015). Physiological and psychological effects of a forest therapy program on middle-aged females. *International Journal of Environmental Research and Public Health*, *12*(12), 15222–15232. https://doi.org/10.3390/ijerph121214984

Oh, B., Lee, K. J., Zaslawski, C., Yeung, A., Rosenthal, D., Larkey, L., & Back, M. (2017). Health and well-being benefits of spending time in forests: Systematic review. *Environmental Health and Preventive Medicine*, *22*(1), 1–11. https://doi.org/10.1186/s12199-017-0677-9

Ohta, H., Maruyama, M., Tanabe, Y., Hara, T., Nishino, Y., Tsujino, Y., Morita, E., Kobayashi, S., & Shido, O. (2008). Effects of redecoration of a hospital isolation room with natural materials on stress levels of denizens in cold season. *International Journal of Biometeorology*, *52*, 331–340. https://doi.org/10.1007/s00484-007-0125-4

Olszewska-Guizzo, A. (2021). Neuroscience-based urban design for mentally healthy cities. *Urban Health and Wellbeing Programme: Policy Briefs: Volume 2*, 13–16. https://doi.org/10.1007/978-981-33-6036-5_3

O'Mara, S. (2005). The subiculum: What it does, what it might do, and what neuroanatomy has yet to tell us. *Journal of Anatomy*, *207*(3), 271–282. https://doi.org/10.1111/j.1469-7580.2005.00446.x

Opel, N., Redlich, R., Grotegerd, D., Dohm, K., Zaremba, D., Meinert, S., Bürger, C., Plümpe, L., Alferink, J., Heindel, W., & others. (2017). Prefrontal brain responsiveness to negative stimuli distinguishes familial risk for major depression from acute disorder. *Journal of Psychiatry and Neuroscience*, *42*(5), 343–352. https://doi.org/10.1503/jpn.160198

Packer, J., & Bond, N. (2010). Museums as restorative environments. *Curator: The Museum Journal*, *53*(4), 421–436. https://doi.org/10.1111/j.2151-6952.2010.00044.x

Pankow, A., Friedel, E., Sterzer, P., Seiferth, N., Walter, H., Heinz, A., & Schlagenhauf, F. (2013). Altered amygdala activation in schizophrenia patients during emotion processing. *Schizophrenia Research*, *150*(1), 101–106. https://doi.org/10.1016/j.schres.2013.07.015

Park, B. J., Tsunetsugu, Y., Kasetani, T., Kagawa, T., & Miyazaki, Y. (2010). The physiological effects of Shinrin-yoku (taking in the forest atmosphere or forest bathing): Evidence from field experiments in 24 forests across Japan. *Environmental Health and Preventive Medicine*, *15*(1), 18–26. https://doi.org/10.1007/s12199-009-0086-9

Park, B.-J., Furuya, K., Kasetani, T., Takayama, N., Kagawa, T., & Miyazaki, Y. (2011). Relationship between psychological responses and physical environments in forest settings. *Landscape and Urban Planning*, *102*(1), 24–32. https://doi.org/10.1016/j.landurbplan.2011.03.005

Peen, J., Schoevers, R. A., Beekman, A. T., & Dekker, J. (2010). The current status of urban-rural differences in psychiatric disorders. *Acta Psychiatrica Scandinavica*, *121*(2), 84–93. https://doi.org/10.1111/j.1600-0447.2009.01438.x

Pignon, B., Szöke, A., Ku, B., Melchior, M., & Schürhoff, F. (2023). Urbanicity and psychotic disorders: Facts and hypotheses. *Dialogues in Clinical Neuroscience*, *25*(1), 122–138. https://doi.org/10.1080/19585969.2023.2272824

Poldrack, R. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, *10*(2), 59–63. https://doi.org/10.1016/j.tics.2005.12.004

Purtle, J., Nelson, K. L., Yang, Y., Langellier, B., Stankov, I., & Roux, A. V. D. (2019). Urban–rural differences in older adult depression: A systematic review and meta-analysis of comparative studies. *American Journal of Preventive Medicine*, *56*(4), 603–613. https://doi.org/10.1016/j.amepre.2018.11.008

Radua, J., Borgwardt, S., Crescini, A., Mataix-Cols, D., Meyer-Lindenberg, A., McGuire, P., & Fusar-Poli, P. (2012). Multimodal meta-analysis of structural and functional brain changes in first episode psychosis and the effects of antipsychotic medication. *Neuroscience & Biobehavioral Reviews*, *36*(10), 2325–2333. https://doi.org/10.1016/j.neubiorev.2012.07.012

Rajoo, K. S., Karam, D. S., & Abdullah, M. Z. (2020). The physiological and psychosocial effects of forest therapy: A systematic review. *Urban Forestry & Urban Greening*, *54*, 1–25. https://doi.org/10.1016/j.ufug.2020.126744

Reese, G., Stahlberg, J., & Menzel, C. (2022). Digital shinrin-yoku: Do nature experiences in virtual reality reduce stress and increase well-being as strongly as similar experiences in a physical forest? *Virtual Reality*, *26*(3), 1245–1255. https://doi.org/10.1007/s10055-022-00631-9

Riches, S., Azevedo, L., Bird, L., Pisani, S., & Valmaggia, L. (2021). Virtual reality relaxation for the general population: A systematic review. *Social Psychiatry and Psychiatric Epidemiology*, *56*(10), 1707–1727. https://doi.org/10.1007/s00127-021-02110-z

Roberts, A. C., & Christopoulos, G. I. (2018). Comment on "Using functional Magnetic Resonance Imaging (fMRI) to analyze brain region activity when viewing landscapes". *Landscape and Urban Planning*, *172*, 25–28. https://doi.org/10.1016/j.landurbplan.2017.12.006

Robinson, J., & Breed, M. (2019). Green prescriptions and their co-benefits: Integrative strategies for public and environmental health. *Challenges*, *10*(1), 1–14. https://doi.org/10.3390/challe10010009

Roe, J., Thompson, C., Aspinall, P., Brewer, M., Duff, E., Miller, D., Mitchell, R., & Clow, A. (2013). Green space and stress: Evidence from cortisol measures in deprived urban communities. *International Journal of Environmental Research and Public Health*, *10*(9), 4086–4103. https://doi.org/10.3390/ijerph10094086

Rojas-Rueda, D., Nieuwenhuijsen, M. J., Gascon, M., Perez-Leon, D., & Mudu, P. (2019). Green spaces and mortality: A systematic review and meta-analysis of cohort studies. *The Lancet Planetary Health*, *3*(11), e469–e477. https://doi.org/10.1016/S2542-5196(19)30215-3

Roozendaal, B., McEwen, B. S., & Chattarji, S. (2009). Stress, memory and the amygdala. *Nature Reviews Neuroscience*, *10*(6), 423–433. https://doi.org/10.1038/nrn2651

Rosa, C. D., Larson, L. R., Collado, S., Cloutier, S., & Profice, C. C. (2023). Gender differences in connection to nature, outdoor preferences, and nature-based recreation among college students in Brazil and the United States. *Leisure Sciences*, *45*(2), 135–155. https://doi.org/10.1080/01490400.2020.1800538

Rosenkranz, J. A., Venheim, E. R., & Padival, M. (2010). Chronic stress causes amygdala hyperexcitability in rodents. *Biological Psychiatry*, *67*(12), 1128–1136. https://doi.org/10.1016/j.biopsych.2010.02.008

Russell, R., Guerry, A. D., Balvanera, P., Gould, R. K., Basurto, X., Chan, K. M. A., Klain, S., Levine, J., & Tam, J. (2013). Humans and nature: How knowing and experiencing nature affect well-being. *Annual Review of Environment and Resources*, *38*(1), 473–502. https://doi.org/10.1146/annurev-environ-012312-110838

Sagi, Y., Tavor, I., Hofstetter, S., Tzur-Moryosef, S., Blumenfeld-Katzir, T., & Assaf, Y. (2012). Learning in the fast lane: New insights into neuroplasticity. *Neuron*, *73*(6), 1195–1203. https://doi.org/10.1016/j.neuron.2012.01.025

Sarkar, C., Webster, C., & Gallacher, J. (2018). Residential greenness and prevalence of major depressive disorders: A cross-sectional, observational, associational study of 94 879 adult UK Biobank participants. *The Lancet Planetary Health*, *2*(4), e162–e173. https://doi.org/10.1016/S2542-5196(18)30051-2

Sehlmeyer, C., Dannlowski, U., Schöning, S., Kugel, H., Pyka, M., Pfleiderer, B., Zwitserlood, P., Schiffbauer, H., Heindel, W., Arolt, V., & others. (2011). Neural correlates of trait anxiety in fear extinction. *Psychological Medicine*, *41*(4), 789–798. https://doi.org/10.1017/S0033291710001248

Shin, W. S., Shin, C. S., Yeoun, P. S., & Kim, J. J. (2011). The influence of interaction with forest on cognitive function. *Scandinavian Journal of Forest Research*, *26*(6), 595–598. https://doi.org/10.1080/02827581.2011.585996

Siegle, G. J., Thompson, W., Carter, C. S., Steinhauer, S. R., & Thase, M. E. (2007). Increased amygdala and decreased dorsolateral prefrontal BOLD responses in unipolar depression: Related and independent features. *Biological Psychiatry*, *61*(2), 198–209. https://doi.org/10.1016/j.biopsych.2006.05.048

Smucny, J., Dienel, S. J., Lewis, D. A., & Carter, C. S. (2022). Mechanisms underlying dorsolateral prefrontal cortex contributions to cognitive dysfunction in schizophrenia. *Neuropsychopharmacology*, *47*(1), 292–308. https://doi.org/10.1038/s41386-021-01089-0

Song, C., Ikei, H., Igarashi, M., Takagaki, M., & Miyazaki, Y. (2015). Physiological and psychological effects of a walk in urban parks in fall. *International Journal of Environmental Research and Public Health*, *12*(11), 14216–14228. https://doi.org/10.3390/ijerph121114216

Song, C., Ikei, H., Kobayashi, M., Miura, T., Taue, M., Kagawa, T., Li, Q., Kumeda, S., Imai, M., & Miyazaki, Y. (2015). Effect of forest walking on autonomic nervous system activity in middle-aged hypertensive individuals: A pilot study. *International Journal of Environmental Research and Public Health*, *12*(3), 2687–2699. https://doi.org/10.3390/ijerph120302687

Song, C., Ikei, H., & Miyazaki, Y. (2018). Physiological effects of visual stimulation with forest imagery. *International Journal of Environmental Research and Public Health*, *15*(2), 1–11. https://doi.org/10.3390/ijerph15020213

Stobbe, E., Sundermann, J., Ascone, L., & Kühn, S. (2022). Birdsongs alleviate anxiety and paranoia in healthy participants. *Scientific Reports*, *12*(1), 1–10. https://doi.org/10.1038/s41598-022-20841-0

Sturm, R., & Cohen, D. (2014). *Proximity to urban parks and mental health*.

Sudimac, S., Drewelies, J., de Weerth, C., & Kühn, S. (2024). *Effects of a walk in a residential natural vs. Usudimacrban environment on objective and subjective stress indicators in mothers and their infants*. PsyArXiv. https://doi.org/10.31234/osf.io/pz83m

Sudimac, S., & Kühn, S. (2022). A one-hour walk in nature reduces amygdala activity in women, but not in men. *Frontiers in Psychology*, *13*, 1–13. https://doi.org/10.3389/fpsyg.2022.931905

Sudimac, S., & Kühn, S. (2023). *WalkGreen: Effects of a one-hour walk in different green spaces on brain*. AsPredicted. https://aspredicted.org/zq92q.pdf

Sudimac, S., & Kühn, S. (2024). *Can a nature walk change your brain? Investigating hippocampal brain plasticity after one hour in a forest*. PsyArXiv. https://doi.org/10.31234/osf.io/g64bq

Sudimac, S., Sale, V., & Kühn, S. (2022). How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature. *Molecular Psychiatry*, *27*(11), 4446–4452. https://doi.org/10.1038/s41380-022-01720-6

Takayama, N., Korpela, K., Lee, J., Morikawa, T., Tsunetsugu, Y., Park, B.-J., Li, Q., Tyrväinen, L., Miyazaki, Y., & Kagawa, T. (2014). Emotional, restorative and vitalizing effects of forest and urban environments at four sites in Japan. *International Journal of Environmental Research and Public Health*, *11*(7), 7207–7230. https://doi.org/10.3390/ijerph110707207

Tang, I.-C., Tsai, Y.-P., Lin, Y.-J., Chen, J.-H., Hsieh, C.-H., Hung, S.-H., Sullivan, W. C., Tang, H.-F., & Chang, C.-Y. (2017). Using functional Magnetic Resonance Imaging (fMRI) to analyze brain region activity when viewing landscapes. *Landscape and Urban Planning*, *162*, 137–144. https://doi.org/10.1016/j.landurbplan.2017.02.007

Taubert, M., Mehnert, J., Pleger, B., & Villringer, A. (2016). Rapid and specific gray matter changes in M1 induced by balance training. *NeuroImage*, *133*, 399–407. https://doi.org/10.1016/j.neuroimage.2016.03.017

Tekgündüz, S. E., Lazoğlu, M., Nailoğlu, M., Apay, S. E., & Tekgündüz, K. Ş. (2023). The relationship of preterm, term, and post-term births to maternal stress and human milk cortisol levels. *Breastfeeding Medicine*, *18*(6), 462–468. https://doi.org/10.1089/bfm.2023.0006

Tomoda, A., Suzuki, H., Rabi, K., Sheu, Y.-S., Polcari, A., & Teicher, M. H. (2009). Reduced prefrontal cortical gray matter volume in young adults exposed to harsh corporal punishment. *NeuroImage*, *47*, T66–T71. https://doi.org/10.1016/j.neuroimage.2009.03.005

Tost, H., Braus, D. F., Hakimi, S., Ruf, M., Vollmert, C., Hohn, F., & Meyer-Lindenberg, A. (2010). Acute D2 receptor blockade induces rapid, reversible remodeling in human cortical-striatal circuits. *Nature Neuroscience*, *13*(8), 920–922. https://doi.org/10.1038/nn.2572

Tost, H., Champagne, F. A., & Meyer-Lindenberg, A. (2015). Environmental influence in the brain, human welfare and mental health. *Nature Neuroscience*, *18*(10), 1421–1431. https://doi.org/10.1038/nn.4108

Tost, H., Reichert, M., Braun, U., Reinhard, I., Peters, R., Lautenbach, S., Hoell, A., Schwarz, E., Ebner-Priemer, U., Zipf, A., & Meyer-Lindenberg, A. (2019). Neural correlates of individual differences in affective benefit of real-life urban green space exposure. *Nature Neuroscience*, *22*(9), 1389–1393. https://doi.org/10.1038/s41593-019-0451-y

Tottenham, N., Hare, T. A., Quinn, B. T., McCarry, T. W., Nurse, M., Gilhooly, T., Millner, A., Galvan, A., Davidson, M. C., Eigsti, I.-M., Thomas, K. M., Freed, P. J., Booma, E. S., Gunnar, M. R., Altemus, M., Aronson, J., & Casey, B. J. (2010). Prolonged institutional rearing is associated with atypically large amygdala volume and difficulties in emotion regulation: Previous institutionalization. *Developmental Science*, *13*(1), 46–61. https://doi.org/10.1111/j.1467-7687.2009.00852.x

Triguero-Mas, M., Gidlow, C. J., Martínez, D., De Bont, J., Carrasco-Turigas, G., Martínez-Íñiguez, T., Hurst, G., Masterson, D., Donaire-Gonzalez, D., Seto, E., Jones, M. V., & Nieuwenhuijsen, M. J. (2017). The effect of randomised exposure to different types of natural outdoor environments compared to exposure to an urban environment on people with indications of psychological distress in Catalonia. *PLOS ONE*, *12*(3), 1–17. https://doi.org/10.1371/journal.pone.0172200

Tsunetsugu, Y., Park, B.-J., Ishii, H., Hirano, H., Kagawa, T., & Miyazaki, Y. (2007). Physiological effects of shinrin-yoku (taking in the atmosphere of the forest) in an old-growth broadleaf forest in Yamagata Prefecture, Japan. *Journal of PHYSIOLOGICAL ANTHROPOLOGY*, *26*(2), 135–142. https://doi.org/10.2114/jpa2.26.135

Tyrväinen, L., Ojala, A., Korpela, K., Lanki, T., Tsunetsugu, Y., & Kagawa, T. (2014). The influence of urban green environments on stress relief measures: A field experiment. *Journal of Environmental Psychology*, *38*, 1–9. https://doi.org/10.1016/j.jenvp.2013.12.005

Ulrich, R. S. (1983). Aesthetic and affective response to natural environment. In *Behavior and the natural environment* (pp. 85–125). Springer. https://doi.org/10.1007/978-1-4613-3539-9_4

Ulrich, R. S., Simons, R. F., Losito, B. D., Fiorito, E., Miles, M. A., & Zelson, M. (1991). Stress recovery during exposure to natural and urban environments. *Journal of Environmental Psychology*, *11*(3), 201–230. https://doi.org/10.1016/S0272-4944(05)80184-7

United Nations, Department of Economic and Social Affairs, Population Division. (2019). *World Urbanization Prospects: The 2018 Revision*. United Nations. https://population.un.org/wup/Publications/Files/WUP2018-Report.pdf

Van den Berg, A. E. (2017). From green space to green prescriptions: Challenges and opportunities for research and practice. *Frontiers in Psychology*, *8*, 1–4. https://doi.org/10.3389/fpsyg.2017.00268

Van den Berg, A. E., & Custers, M. H. G. (2011). Gardening promotes neuroendocrine and affective restoration from stress. *Journal of Health Psychology*, *16*(1), 3–11. https://doi.org/10.1177/1359105310365577

Van den Berg, M., Wendel-Vos, W., Van Poppel, M., Kemper, H., Van Mechelen, W., & Maas, J. (2015). Health benefits of green spaces in the living environment: A systematic review of epidemiological studies. *Urban Forestry & Urban Greening*, *14*(4), 806–816. https://doi.org/10.1016/j.ufug.2015.07.008

Van Os, J., Kenis, G., & Rutten, B. P. F. (2010). The environment and schizophrenia. *Nature*, *468*(7321), 203–212. https://doi.org/10.1038/nature09563

Vassos, E., Pedersen, C. B., Murray, R. M., Collier, D. A., & Lewis, C. M. (2012). Meta-analysis of the association of urbanicity with schizophrenia. *Schizophrenia Bulletin*, *38*(6), 1118–1123. https://doi.org/10.1093/schbul/sbs096

Veitch, J., Timperio, A., Salmon, J., Hall, S. J., Abbott, G., Flowers, E. P., & Turner, A. I. (2022). Examination of the acute heart rate and salivary cortisol response to a single bout of walking in urban and green environments: A pilot study. *Urban Forestry & Urban Greening*, *74*, 1–8. https://doi.org/10.1016/j.ufug.2022.127660

Wang, X., Rodiek, S., Wu, C., Chen, Y., & Li, Y. (2016). Stress recovery and restorative effects of viewing different urban park scenes in Shanghai, China. *Urban Forestry & Urban Greening*, *15*, 112–122. https://doi.org/10.1016/j.ufug.2015.12.003

Wass, S. V., Smith, C. G., Stubbs, L., Clackson, K., & Mirza, F. U. (2021). Physiological stress, sustained attention, emotion regulation, and cognitive engagement in 12-month-old infants from urban environments. *Developmental Psychology*, *57*(8), 1179–1194. https://doi.org/10.1037/dev0001200

White, M. P., Elliott, L. R., Grellier, J., Economou, T., Bell, S., Bratman, G. N., Cirach, M., Gascon, M., Lima, M. L., Lõhmus, M., Nieuwenhuijsen, M., Ojala, A., Roiko, A., Schultz, P. W., Van Den Bosch, M., & Fleming, L. E. (2021). Associations between green/blue spaces and mental health across 18 countries. *Scientific Reports*, *11*(1), 1–12. https://doi.org/10.1038/s41598-021-87675-0

White, M. P., Hartig, T., Martin, L., Pahl, S., Van Den Berg, A. E., Wells, N. M., Costongs, C., Dzhambov, Angel. M., Elliott, L. R., Godfrey, A., Hartl, A., Konijnendijk, C., Litt, J. S., Lovell, R., Lymeus, F., O'Driscoll, C., Pichler, C., Pouso, S., Razani, N., … Van Den Bosch, M. (2023). Nature-based biopsychosocial resilience: An integrative theoretical framework for research on nature and health. *Environment International*, 1–66. https://doi.org/10.1016/j.envint.2023.108234

Wilson, E. O. (1986). *Biophilia*. Harvard university press.

Wood, L., Hooper, P., Foster, S., & Bull, F. (2017). Public green spaces and positive mental health – investigating the relationship between access, quantity and types of parks and mental wellbeing. *Health & Place*, *48*, 63–71. https://doi.org/10.1016/j.healthplace.2017.09.002

World Health Organization. (2016). *Urban green spaces and health*. World Health Organization. Regional Office for Europe.

Wright, I. C., Sham, P., Murray, R. M., Weinberger, D. R., & Bullmore, E. T. (2002). Genetic contributions to regional variability in human brain structure: Methods and preliminary results. *Neuroimage*, *17*(1), 256–271. https://doi.org/10.1006/nimg.2002.1163

Yang, T. T., Simmons, A. N., Matthews, S. C., Tapert, S. F., Frank, G. K., Max, J. E., Bischoff-Grethe, A., Lansing, A. E., Brown, G., Strigo, I. A., & others. (2010). Adolescents with major depression demonstrate increased amygdala activation. *Journal of the American Academy of Child & Adolescent Psychiatry*, *49*(1), 42–51. https://doi.org/10.1097/00004583-201001000-00008

Zhao, Z., Gong, Y., Li, Y., Zhang, L., & Sun, Y. (2021). Gender-Related Beliefs, Norms, and the Link With Green Consumption. *Frontiers in Psychology*, *12*, 1–13. https://doi.org/10.3389/fpsyg.2021.710239

Zijlema, W. L., Avila-Palencia, I., Triguero-Mas, M., Gidlow, C., Maas, J., Kruize, H., Andrusaityte, S., Grazuleviciene, R., & Nieuwenhuijsen, M. J. (2018). Active commuting through natural environments is associated with better mental health: Results from the PHENOTYPE project. *Environment International*, *121*, 721–727. https://doi.org/10.1016/j.envint.2018.10.002

Appendices

A: Paper I

Sudimac, S., Sale, V., & Kühn, S. (2022). How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature. *Molecular Psychiatry*, 27(11), 4446–4452. https://doi.org/10.1038/s41380-022-01720-6

ARTICLE OPEN

How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature

Sonja Sudimac [1,2,3]✉, Vera Sale [1,2] and Simone Kühn [1,2,4,5]

Since living in cities is associated with an increased risk for mental disorders such as anxiety disorders, depression, and schizophrenia, it is essential to understand how exposure to urban and natural environments affects mental health and the brain. It has been shown that the amygdala is more activated during a stress task in urban compared to rural dwellers. However, no study so far has examined the causal effects of natural and urban environments on stress-related brain mechanisms. To address this question, we conducted an intervention study to investigate changes in stress-related brain regions as an effect of a one-hour walk in an urban (busy street) vs. natural environment (forest). Brain activation was measured in 63 healthy participants, before and after the walk, using a fearful faces task and a social stress task. Our findings reveal that amygdala activation decreases after the walk in nature, whereas it remains stable after the walk in an urban environment. These results suggest that going for a walk in nature can have salutogenic effects on stress-related brain regions, and consequently, it may act as a preventive measure against mental strain and potentially disease. Given rapidly increasing urbanization, the present results may influence urban planning to create more accessible green areas and to adapt urban environments in a way that will be beneficial for citizens' mental health.

Molecular Psychiatry (2022) 27:4446–4452; https://doi.org/10.1038/s41380-022-01720-6

INTRODUCTION

The human brain is shaped by its surroundings. Increasing urbanization has been one of the recent major changes in our environment, resulting in more than half of the world's population currently living in cities, projected to increase to 68% by 2050 [1].

Even though urbanization has many advantages, living in a city is a well-known risk factor for mental health [2]. Mental health problems like anxiety, mood disorders, major depression, and schizophrenia are up to 56% more common in urban compared to rural environments [3]. It has been suggested that urban upbringing is the most important environmental factor for developing schizophrenia [4], accounting for more than 30% of schizophrenia incidence [5]. Since there is a consistent dose-response relationship between schizophrenia and urban environment, even when controlling for possible confounders such as sociodemographic factors, family history, drug abuse, and size of social network [4], the hypothesis is that urban environment is related to higher schizophrenia incidence through increased social stress [6, 7].

On the other hand, exposure to nature provides attentional restoration and stress relief [8, 9]. The biophilia hypothesis states that humans feel an innate tendency to connect with nature since this attitude is rooted in our evolutionary history [10, 11]. Research about the beneficial effects of nature has been mainly motivated by two theoretical frameworks – Attention Restoration Theory (ART) [12] and Stress Recovery Theory (SRT) [13], that explain the psychological benefits of nature from different perspectives. ART focuses on cognitive restoration through nature exposure. The notion is that nature invokes involuntary attention allowing voluntary attention processes to recover [14]. SRT, on the other hand, emphasizes affective responses in contact with nature, that lead to restoration. According to SRT, the restorative process is related to the stress-reducing capacity of natural environments that involves an increase in positive emotions as well as a decrease in arousal and negative emotions such as fear [9, 13].

A growing body of empirical research has demonstrated the cognitive and affective benefits of exposure to natural environments. Spending time in nature can improve working memory capacity [15], restore directed attention [8] as well as reduce negative emotions and stress [16–18]. The evidence of nature's beneficial effects on stress has been observed not only in psychological assessments, but also in physiological indicators of stress, namely in decreases in heart rate, blood pressure, and stress-related hormone cortisol [19, 20].

Even though the beneficial effects of nature exposure have been repeatedly shown, the neural underpinnings of these effects are unknown. In a seminal cross-sectional study, the amygdala has been shown to be more activated during a social stress task in urban compared to rural dwellers [21]. Nevertheless, intervention studies are needed to demonstrate the causal effects of natural and urban environments on the brain. In a single functional magnetic resonance imaging (fMRI) intervention study conducted

[1]Max Planck Institute for Human Development, Lise Meitner Group for Environmental Neuroscience, Lentzeallee 94, 14195 Berlin, Germany. [2]Max Planck Institute for Human Development, Max Planck Dahlem Campus of Cognition (MPDCC), Lentzeallee 94, 14195 Berlin, Germany. [3]Max Planck Institute for Human Development, International Max Planck Research School on the Life Course (LIFE), Lentzeallee 94, 14195 Berlin, Germany. [4]University Medical Center Hamburg-Eppendorf, Department of Psychiatry and Psychotherapy, Martinistr. 52, 20251 Hamburg, Germany. [5]Max Planck UCL Centre for Computational Psychiatry and Ageing Research Berlin, Germany and London, UK, Lentzeallee 94, 14195 Berlin, Germany. ✉email: sudimac@mpib-berlin.mpg.de

Received: 26 November 2021 Revised: 18 July 2022 Accepted: 22 July 2022
Published online: 5 September 2022

so far it was shown that a 90-minute walk in nature decreased self-reported rumination and activity in the subgenual prefrontal cortex (sgPFC), associated with rumination, whereas there was no change after the urban walk [22].

However, to the best of our knowledge, there has been no fMRI intervention study examining the causal effects of exposure to urban vs. natural environments on stress-related brain regions. And importantly, the previous findings do not disentangle whether stress-relief after being in nature is the result of exposure to the natural environment itself or merely of the absence of detrimental urban effects. To address these questions, we conducted an fMRI intervention study investigating brain activity before and after a one-hour exposure to natural versus urban environments. We hypothesized that stress-related brain regions would be less activated after exposure to the natural compared to the urban environment, relative to the baseline activation before the walk. A-priori defined and preregistered (https://aspredicted.org/tm629.pdf) brain regions of interest (ROI) included amygdala, anterior cingulate cortex (ACC), and dorsolateral prefrontal cortex (dlPFC).

MATERIALS AND METHODS

Participants

Participants were recruited from the Castellum database of the Max Planck Institute for Human Development in Berlin, via mailing lists of universities in Berlin, and through the online platform *ebay-kleineanzeigen.de*. Participants were told that they would take part in an MRI study and that they would go for a walk, but were not informed about the research question of the study. All participants were fluent in the German language, right-handed, and were not diagnosed with any psychological or neurological disorders. A sample size estimation using G*Power resulted in the need of 54 participants to enable a medium effect size. We tested 9 participants more to ensure that potential drop outs would not reduce the sample size below the number we decided on. The final sample consisted of 63 participants (29 females, total mean age = 27.21 years, $SD = 6.61$, age-range = 18−47 years). The participants were pseudo-randomly assigned either to a nature (32 participants) or an urban walk (31 participants), while controlling that men and women were equally distributed in both environments. During randomization, it was also controlled that the number of afternoon walks were equally distributed between conditions. An overview over the control variables in the two conditions is shown in Supplementary Table 1.

The study was approved by the Local Psychological Ethical Committee at the Center for Psychosocial Medicine at University Medical Center Hamburg-Eppendorf in Hamburg, Germany (LPEK-0054). We obtained written informed consent from all participants and they received monetary compensation for the participation in the study.

Study procedure

The experiment was conducted in late summer/fall 2019 during daylight, between 10:00 a.m. and 5:00 p.m. The flowchart of the study procedure is shown in Fig. 1. Upon arrival, participants signed the informed consent, filled out the questionnaires, and performed a working memory task. Subsequently, the participants underwent an fMRI scanning procedure that included questions on rumination [23], the Fearful Faces Task (FFT) [24], and the Montreal Imaging Stress Task (MIST) [25]. The MIST was administered in order to induce social stress, since the SRT [13] hypothesizes that nature's restorative potential is most evident when the individual is in a stressed state. The order of the FFT and MIST was counterbalanced between subjects, however, the order was the same within subjects, at pretest and posttest.

After the scanning session, participants were randomly assigned to a 60-minute walk in either a natural or urban environment (Fig. 2). Even though the definition and also the dichotomy of 'natural' and 'urban' environment has been an object of debate [26], the 'natural environment' we refer to is an urban forest, the largest green area in the city of Berlin (Grunewald forest; Fig. 2b), whereas the 'urban environment' refers to a busy street in one of the city centers in Berlin with shopping malls (Schloßstraße; Fig. 2c). As recommended in the recent review [27], geographic locations of the walk and the landscape features of the environments are reported (see Supplementary information).

The participants were shown the exact walk route on a map (straight path) and they were collected at the lab and brought by taxi to the starting point of the walk. They carried a mobile phone that logged participants' global positioning system (GPS) data during the walk, to ensure that they walked the intended route (Fig. 2a). During the walk, participants were equipped with an Empatica E4 (Empatica S.r.l, Milan, Italy), a wristband measuring electrodermal activity (EDA), heart rate variability (HRV), and heart rate, as physiological indicators of stress. Participants went on the walk alone and were instructed not to enter shops or use their mobile phones, to avoid potential distraction. They were given a bagged lunch that they could eat during the walk. After 30 min, as an alarm signal was generated by the phone, they turned around and continued the walk back to the starting point. Here they were picked up by a taxi and brought back to the lab.

After the walk the same fMRI scanning procedure was repeated, with one additional stress-inducing task, the Social-Evaluative Threat task (SET) [28], a modified version of the Trier Social Stress Test [29], meant to induce social stress and presented only after the walk, since we reasoned that the participants would not have believed the cover story twice (for detailed SET task procedure see Supplementary information). Additionally, the participants reported the level of restored attention after the walk via a questionnaire. Finally, the participants were debriefed and informed about the aim of the study. Within the scope of this article, we report on the fMRI results on the FFT and the MIST.

Functional imaging paradigms

Fearful Faces Task (FFT). An adapted version of the Fearful Faces Task (FFT) [24] was used, designed to measure amygdala activity during fearful and neutral facial expressions. While in the MRI scanner, participants were presented with stimuli, consisting of 15 male and 15 female faces, each depicting fearful (Fear condition; Fig. 3 bottom left) or neutral facial expression (Neutral condition; Fig. 3 bottom right). Both fearful and neutral facial expressions were shown either for 1000 ms (unmasked stimuli) or for 17 ms followed by a mask with neutral facial expression presented for 983 ms (masked stimuli). Since the amygdala has been shown to respond to masked stimuli even when most of the participants were not aware of their presence [30–32], we used masked stimuli in order to exploratorily examine whether the degree of conscious perception had an effect on amygdala activity. However, we did not have the time to perform a perceptual control test and therefore we have no proof that the masked stimuli were actually processed outside of the participants' awareness.

We used the set of 60 stimuli from the FACES database by the Max Planck Institute for Human Development in Berlin [33], consisting of face photographs on a gray background, matched on size and luminance. We used the FACES database because it provides a large set of validated high-resolution photographs with natural facial expressions that vary by gender, age, and emotion. The fMRI paradigm consisted of 22 blocks with 6 pictures interleaved with a 200 ms break between pictures. Each block was followed by a white fixation cross presented for 9 s. In order to monitor the participants' attention, the fixation cross was red on two occasions, and participants were instructed to press the button on the response box as soon as they would see the red cross on the screen. The order of the stimuli was randomized within 10 versions of the FFT, and the task version was introduced in the fMRI data analysis as a covariate. The whole task sequence lasted 8 minutes and 28 s. The task was presented via a projector and mirror system and the participants answered using a response box. The FFT was presented using software Presentation (version: 19.0) and the code for the task used in this study is openly available at https://osf.io/5m2qv.

Montreal Imaging Stress Task (MIST). The Montreal Imaging Stress Task (MIST) [25] is a computerized fMRI-adapted paradigm, based on the Trier Social Stress Test [29], with an aim to induce social stress, in which participants solve mental arithmetic tasks with a time limit designed to be just beyond the participant's cognitive capacities. The MIST consisted of three different conditions: Experimental, Control, and Rest (Supplementary Fig. 1).

In the Experimental condition, the information about individual performance and a fake-average performance of all participants was graphically presented after each response. This fake-average performance was consistently considerably better than the individual performance in order to induce social stress. In the Control condition, the mental arithmetic tasks had the same level of difficulty as in the Experimental condition, but the participant's performance as well as the fake-average

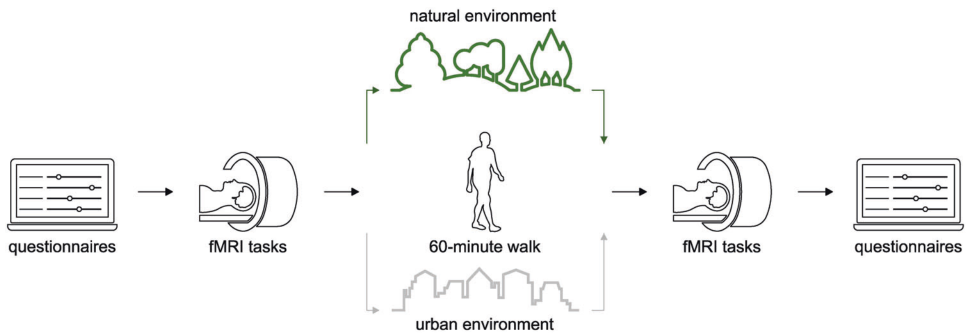


Fig. 1 Flowchart of the study procedure. Before the walk participants filled out questionnaires and underwent the fMRI scanning procedure, which included the Fearful Faces Task and the Montreal Imaging Stress Task. Subsequently, each participant was randomly assigned to a 60-min walk, in either a natural or urban environment. After the walk, the participants underwent the fMRI scanning procedure again and filled out the questionnaires.

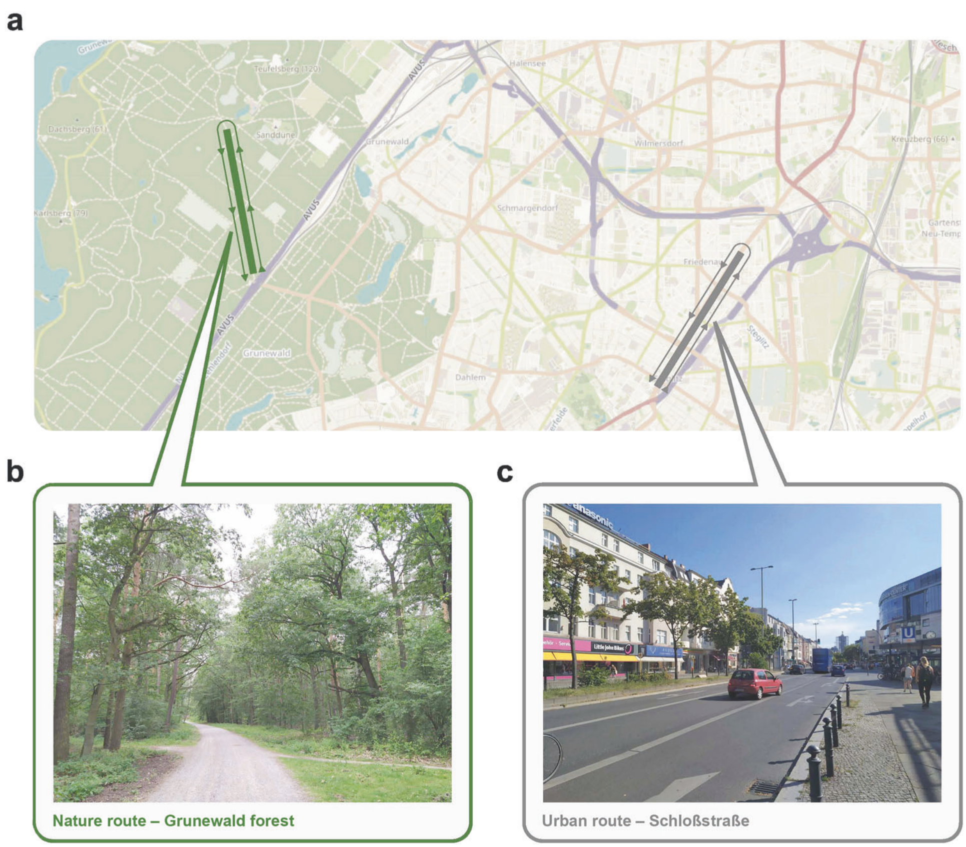


Fig. 2 Location of the nature and urban walk. a GPS data of two participants during the walk in the natural environment (Berlin, Grunewald) and the urban environment (Berlin, Schloßstraße) displayed on the OpenStreetMap (https://www.openstreetmap.org). **b** Sample picture of the walk in the natural environment. **c** Sample picture of the walk in the urban environment.

performance of all participants was not displayed and there was no time limit for solving the task. In the Rest condition, treated as a baseline, no task was displayed and the participants were asked to simply passively look at the screen [25]. For detailed MIST procedure see Supplementary information.

Magnetic Resonance Imaging

Data acquisition. All images were acquired on a Siemens Tim Trio 3 T scanner (Erlangen, Germany) using a 32-channel head coil. The T1-weighted images were obtained using a three-dimensional T1-weighted magnetization prepared gradient-echo sequence (MPRAGE; repetition time (TR) = 2500 ms; echo time (TE) = 4.77 ms; TI = 1100 ms, acquisition matrix = $256 \times 256 \times 192$, flip angle = 7°; 1 x 1 x 1 mm^3 voxel size). Whole brain functional images were collected using a T2*-weighted echo-planar imaging (EPI) sequence sensitive to BOLD contrast (TR = 2000 ms, TE = 30 ms, acquisition matrix = $216 \times 216 \times 129$, flip angle = 80°, slice thickness = 3.0 mm, distance factor = 20%, FOV = 216 mm, $3 \times 3 \times 3$ mm^3 voxel size, 36 axial slices, using GRAPPA).

Data preprocessing. Functional imaging data were preprocessed and analyzed using Statistical Parametric Mapping software (SPM12; https://www.fil.ion.ucl.ac.uk/spm/software/spm12/). EPIs were corrected for slice timing and head motion and transformed into the stereotactic normalized standard space of the Montreal Neuroimaging Institute (MNI) using the unified segmentation algorithm. Finally, spatial smoothing with a 6-mm full width at half-maximum (FWHM) Gaussian kernel was performed. The

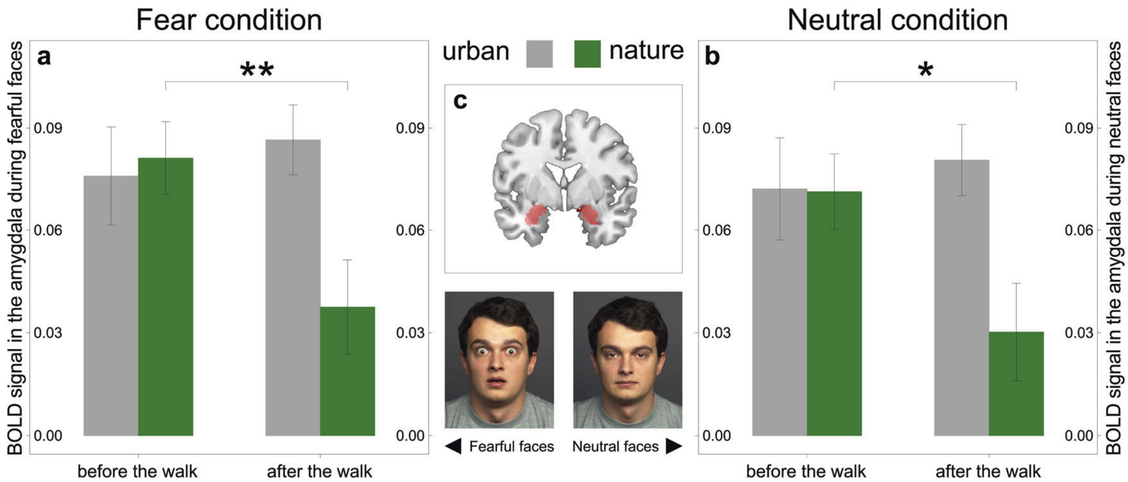


Fig. 3 Bilateral amygdala activity during the Fearful Faces Task before and after the walk in the urban and in the natural environment. a a Bilateral amygdala activity while watching fearful faces (Fear condition) decreased after the walk in the natural environment. **b** Bilateral amygdala activity while watching neutral faces (Neutral condition) decreased after the walk in the natural environment. **c** Region of interest, the bilateral amygdala as defined in Automated Anatomic Labelling Atlas 2. Bottom: Stimuli in the Fearful Faces Task showing fearful facial expression, within the Fear condition (left) and neutral facial expression within the Neutral condition (right). Note: BOLD stands for Blood-Oxygen Level-Dependent; Significant differences are indicated with asterisks (**P* < 0.05; ***P* < 0.01); error bars represent one standard error of the mean.

voxel size was not changed during preprocessing but kept in the original acquisition dimension ($3 \times 3 \times 3$ mm^3).

Data analysis. At the first level analysis of the FFT estimates of functional activation during conditions (unmasked Fear, unmasked Neutral, masked Fear, masked Neutral, Response) were obtained using an event-related paradigm. A high-pass filter (cut-off 128 s) was applied. Subsequently, a whole brain analysis was performed, using flexible factorial design with a focus on the interaction of environment (urban vs. natural) and time (before vs. after the walk). Both interaction contrasts were analyzed (Fear > Neutral and Neutral > Fear), using family-wise error (FEW) correction with a threshold at $P < 0.05$, and no significant clusters survived. Additionally, in order to perform a whole brain analysis with less rigorous threshold, the contrasts were thresholded at $P < 0.001$, uncorrected while controlling for multiple testing on the cluster level using 3DClutSim in AFNI (Analysis of Functional Neuroimages) [34] and again no significant clusters survived.

We then used a ROI-based approach, based on our a priori hypothesis, focusing on ROI amygdala, ACC (both derived from the Automated Anatomic Labelling atlas 2 [35], https://www.gin.cnrs.fr/en/tools/aal/), and dlPFC (left and right frontal superior gyrus), derived from the SPM Anatomy Toolbox [36], using WFU PickAtlas (https://www.nitrc.org/projects/wfu_pickatlas). Volume of the bilateral amygdala was 3744 mm^3, dlPFC volume was 79,968 mm^3, and ACC volume was 21,704 mm^3. We extracted mean BOLD signal from a time window of 4–6 s after stimulus onset across all voxels within each ROI using a Matlab script based on the marsbar toolbox (version 0.44 [37]). We reasoned that the intervention, namely a one-hour walk, would globally affect the stress level and therewith stress-related brain activity, not only when contrasting the Fear > Neutral condition. To test this, we examined activity of each ROI (bilateral amygdala, dlPFC, and ACC) in Fear and Neutral condition separately. Since the results in both conditions were similar, we also examined pooled ROI activity of Fear and Neutral condition. We averaged data from unmasked and masked stimuli, because the results were similar.

We conducted a two-way mixed ANOVA with environment as a between-subject factor (urban vs. natural) and time as a within-subject factor (before vs. after the walk), in the Fear and Neutral condition separately, and also in the ROI pooled activity of Fear and Neutral conditions, while focusing on environment-by-time interaction. Two-tailed post-hoc *t*-tests were performed within the urban and the natural environment to examine the differences in ROI activity before and after the walk in each environment as well as separately within Fear and Neutral conditions, and the pooled activity of the latter conditions. Additionally, the amygdala subregions (centromedial and laterobasal amygdala) were derived from an atlas of the SPM Anatomy Toolbox [36] and the two-way mixed ANOVA was performed in the same ways as described above.

At the first level analysis of the MIST we obtained estimates of functional activation during the three conditions within a block-design paradigm (Experimental, Control, and Rest) and applied a high-pass filter (cut-off 520 s). We first performed a whole brain analysis, using flexible factorial model and focusing on the interaction of environment (urban vs. natural) and time (before vs. after the walk). Both interaction contrasts (Exp > Cont and Cont > Exp) were analyzed, using family-wise error correction with a threshold at $P < 0.05$ and no significant clusters survived. Subsequently, to present a more lenient thresholding, the contrasts were thresholded at $P < 0.001$, uncorrected while controlling for multiple testing on the cluster level using 3DClustSim in AFNI [34]. Significant clusters within the Experimental > Control contrast are shown in the Supplementary Table 2. No significant clusters survived within the Control > Experimental contrast.

To analyze ROI activity within the MIST, we extracted the beta values within each ROI separately for the contrasts Experimental > Rest and Control > Rest, in order to obtain the beta values in the Experimental and Control condition relative to baseline (Rest condition). Subsequently, a 2 x 2 x 2 mixed ANOVA was conducted with condition (Experimental vs. Control) and environment as a between-subject factor (urban vs. natural) and time as a within-subject factor (before vs. after the walk) for the amygdala activity, also focusing on environment-by-time interaction. Additionally, and in accordance with how the FFT data was analyzed, post-hoc *t*-tests were conducted with pooled amygdala activity of the Experimental and Control condition as a dependent variable in order to examine if the environment-by-time interaction was driven by a change in the amygdala activity after the walk in the urban or in the natural environment.

Behavioural data and Physiological data are reported in the Supplementary information.

RESULTS

As hypothesized, we observed a significant environment-by-time interaction in bilateral amygdala in the Fear [$F(1,61) = 6.11$, $P = 0.016$, $\eta^2_g = 0.04$; Fig. 3a] as well as in the Neutral condition [$F(1,61) = 4.86$, $P = 0.031$, $\eta^2_g = 0.03$; Fig. 3b]. Moreover, a significant environment-by-time interaction was likewise observed when bilateral amygdala activity within both Fear and Neutral conditions was pooled [$F(1,61) = 5.81$, $P = 0.019$, $\eta^2_g = 0.04$]. There was no significant time-by-environment interaction neither in ACC or dlPFC in the FFT in the Fear condition (Supplementary Table 3), Neutral condition (Supplementary Table 4), nor in the pooled activity of the Fear and Neutral conditions (Supplementary Table 5).

To investigate whether the environment-by-time interaction in amygdala activity was mostly driven by an increase in the urban environment or by a decrease in the natural environment, we conducted follow-up *t*-tests. The two-tailed paired post-hoc *t*-tests for pooled activity during the Fear and Neutral condition revealed that amygdala activity was stable in the urban environment [$t(30) = -0.67$, $P = 0.506$], whereas there was a significant decrease in amygdala activity after the walk in nature [$t(31) = 2.62$, $P = 0.014$]. A two-tailed paired post-hoc *t*-test also showed a decrease in amygdala activity after the walk in natural environment when tested separately within the Fear [$t(31) = 2.77$, $P = 0.009$; Fig. 3a] and the Neutral condition [$t(31) = 2.37$, $P = 0.024$; Fig. 3b]. Therefore, the environment-by-time interaction was driven by a significant decrease in amygdala activity after the walk in nature (Fig. 3). Additionally, we observed that the interaction in amygdala activation was lateralized and mostly driven by the activity in the right amygdala [$F(1,61) = 7.00$, $P = 0.010$, $\eta^2_g = 0.04$].

Interestingly, the analysis of bilateral amygdala activity only during masked stimuli as well revealed a significant environment-by-time interaction [$F(1,61) = 5.58$, $P = 0.021$, $\eta^2_g = 0.03$], showing a decrease after the exposure to the natural environment [$t(31) = 2.65$, $P = 0.012$].

Exploratorily, we tested different subregions of the amygdala separately and observed a significant environment-by-time interaction in the basolateral amygdala [$F(1,61) = 5.17$, $P = 0.026$, $\eta^2_g = 0.03$; Supplementary Fig. 2], likewise driven by a decrease in its activity after the walk in nature [$t(31) = 1.98$, $P = 0.057$].

As hypothesized and in the same direction as in the FFT, we observed a significant environment-by-time interaction in amygdala activity in pooled Experimental and Control condition in the MIST [$F(1,61) = 5.07$, $P = 0.028$, $\eta^2_g = 0.02$; Supplementary Fig. 3]. Likewise in the FFT, two-tailed paired post-hoc *t*-tests within the MIST revealed that the interaction was driven by a decrease in amygdala activity after the walk in nature [$t(31) = 1.88$, $P = 0.070$], whereas amygdala activity remained stable after the walk in the urban environment [$t(30) = -1.28$, $P = 0.211$]. In the MIST, as in the FFT, there was no time-by-environment interaction in ACC or dlPFC (Supplementary Table 6).

There was no significant environment-by-time interaction in self-report measures or in the cognitive task (Supplementary Tables 7, 8) nor in physiological indicators of stress (Supplementary Table 9). However, as predicted, perceived restorativeness was higher after the nature walk than after the urban walk [$Z = -3.85$, $P < 0.001$, $r = 0.49$; Supplementary Fig. 4 and Supplementary Table 10]. Moreover, participants who went for a walk in nature reported that they enjoyed the walk more [$Mdn = 92$, $IQR = 20.5$], compared to the participants who went for an urban walk [$Mdn = 70$, $IQR = 40.5$, $Z = -2.87$, $P = 0.004$, $r = 0.37$].

DISCUSSION

Living in an urban environment has been associated with mental health problems, like anxiety disorders, depression, and schizophrenia, with urban upbringing being the most important environmental factor for developing schizophrenia [3, 4]. To investigate causal effects of urban and natural environments on the brain, we conducted an intervention study that examined changes in stress-related brain regions after a one-hour walk in an urban vs. natural environment. Furthermore, we aimed to explore whether stress-relief after exposure to nature is a result of the natural environment itself or of the mere absence of disadvantageous urban effects.

In line with our hypothesis, we observed that amygdala activity decreased after the walk in nature, whereas it remained the same after the walk in the urban environment. We interpret this as evidence showing that nature is indeed able to restore individuals from stress, and as a lack of evidence that the administered urban exposure additionally heightens amygdala activity.

We observed a decrease in amygdala activity after the walk in nature not only during fearful, but also during neutral faces in the FFT. The bilateral amygdala has been shown to respond to both fearful and neutral faces [38], although it is prominently reported that subtracting brain activity during neutral faces from that during fearful faces results in amygdala activity [24, 39, 40]. We speculate that the effect of exposure to nature was rather a general effect that affected the amygdala by increasing its threshold for activation, consequently leading to an interaction effect during both fearful and neutral faces.

Furthermore, we found that amygdala activity during masked stimuli showed the same effect as during unmasked stimuli, namely, it decreased after the walk in nature, whereas it remained stable after the walk in the urban environment. These results are in accordance with previous evidence showing that the amygdala can be activated in response to masked stimuli that participants were not aware of, in absence of cortical processing [30, 31] and suggest that the beneficial effect of nature exposure on stress may occur outside of our awareness.

Interestingly, we observed that the environment-by-time interaction effect was mostly driven by the activity in right amygdala, which is in line with the previous study showing lower amygdala activity in rural compared to urban dwellers, also lateralized to the right amygdala [21]. Exploratorily, we examined amygdala subregions separately and found an environment-by-time interaction (the activity remaining stable after the urban walk, whereas descriptively decreasing after the nature walk) in the basolateral amygdala activity, a subregion that has previously been reported in the context of fear conditioning [41] and to be activated during anxiety [42].

As predicted, and in line with the results on the FFT, we observed a significant environment-by-time interaction in amygdala activity also in the social stress task, the MIST, with amygdala activity remaining stable after the walk in the urban environment and descriptively decreasing after the walk in nature. These results indicate that predicted effects of walks in natural environments on stress-related brain regions occur also under conditions of social stress. The same pattern of amygdala activity after the exposure to the natural environment observed in both tasks, the FFT and the MIST, suggests that a one-hour walk in nature may have had a global beneficial effect on amygdala activity resulting in increasing amygdala's threshold for activation, regardless of the task at hand. Since environment-by-time interaction was not observed in the ACC or dlPFC neither in the FFT nor in the MIST, the data imply that the amygdala may be a key stress-related brain region where the environment has an effect.

A possible explanation for why there was no observed change in behavioural measures after the walk may lie in the fact that the posttest questionnaires referred to mood and stress experienced during the previous hour, when participants were undergoing the fMRI stress-inducing paradigm. Therefore, we believe that the questionnaires were not able to capture the effect of the walk, but rather the effect of the stress-inducing paradigm. In future studies, behavioural measures should be administered in a short form as soon as participants come back from the walk, in order to capture the effect of the walk within both the questionnaires and the fMRI paradigm.

However, perceived restorativeness, referring to restored attention during the walk, was reported to be higher after the walk in nature than after the urban walk, which is in line with the ART [14] and previous studies [8] showing that natural environments have restorative benefits on attention. Moreover, participants who went for a nature walk enjoyed the walk more than those who went for a walk in the urban environment, a finding that is consistent with participants' higher restorativeness as well as lower amygdala activity after the walk in nature.

According to ART, natural environments restore cognition, whereas within the SRT framework, nature-induced restoration is related to recovery from stress. Even though ART and SRT are complementary theoretical frameworks [8, 9], in the context of this study, ART would emphasize restored cognition and therefore effects in cognitive brain areas, whereas SRT would focus rather on the importance of stress-related brain areas. Since the results show a decrease in stress-related brain areas (bilateral amygdala) after the walk in nature, and no change in cognition-related brain areas (dlPFC and ACC), the brain data of the present study are more strongly in line with SRT.

To the best of our knowledge, this is the first study to demonstrate the causal effects of acute exposure to a natural vs. urban environment on stress-related brain regions, disentangling positive effects of nature from negative effects of city. We demonstrated that amygdala activation decreased during a stress task after nature exposure, whereas it remained stable after urban exposure. This strongly argues in favor of the salutogenic effects of nature as opposed to urban exposure causing additional stress.

The results presented may reveal the mechanism behind the long-term effects of the environment on stress-related brain regions. The decrease in amygdala activity as a result of acute exposure to nature might be a mechanism explaining lower amygdala activity during stress in rural dwellers [21] and higher structural amygdala integrity in citizens who live close to urban forests [43]. Repeated exposures to nature may beneficially affect amygdala by increasing its threshold for activation, resulting in lower amygdala activity during stress and higher amygdala integrity in habitants who live close to natural environments.

Detrimental effects of urban environments related to higher schizophrenia incidence in cities, like social stress, might be attenuated with exposure to natural environments through decreased stress-related amygdala activation. Since schizophrenia has been related to urban upbringing [4] and amygdala alterations [44], spending time in urban nature (green prescription) and consequently decreasing amygdala engagement may buffer the disadvantageous impact of the city and serve as a preventive measure against developing schizophrenia. Higher association between urbanicity and schizophrenia in recent birth cohorts and rapidly increasing urbanization suggest that effects of urban environment may increase in the future [4], underlining the responsibility of urban planning to focus on modifying current and future cities to provide accessible green spaces in order to improve citizens' mental health.

One of the limitations of the study is the lack of evidence that the masked facial stimuli in the FFT were not consciously perceived, since we have not explicitly tested for this. We would recommend that future studies perform a perceptual control task in order to ensure that participants did not consciously perceive the masked stimuli. Secondly, it is not clear which aspects of nature are driving the effect of the decrease in amygdala activation after exposure to natural environment. Therefore, future studies should aim to pinpoint specific features of nature that are beneficial and drive the decrease in amygdala activity (e.g., green color, sound, odors, terpenes etc.) in order to understand why nature induces restorative processes and, consequently, to make nature-based therapy more efficient. Thirdly, even though the Grunewald forest path where the participants went for a walk is isolated from the city, participants might have seen other people engaged in spare time activities, such as walking or exercising, which could have contributed to higher relaxation and lower amygdala activity after the walk in nature compared to the urban walk. Hence, future studies should control for number of people encountered during the walk as well as for their affective state, since this may be different in natural and urban environments. Fourthly, different natural environments may have different effects on participants (e.g., a forest could elicit fear instead of relaxation [45] and walking in a tended forest may have a more positive impact on well-being than walking in a wild forest [46]). Therefore, future studies should examine changes in stress-related brain regions after exposure to different types of natural environments, for example to an urban park or a botanical garden. Finally, since the assignment of meaning to nature likely differs across cultures [47, 48], future research should try to include participants from different cultural backgrounds in order to examine whether the beneficial effects of nature on stress-related brain regions differ across cultures.

To conclude, our results demonstrate that exposure to nature for one hour decreases amygdala activity and can have salutogenic effects on brain regions related to stress. This suggests that going for a walk in nature may buffer detrimental effects of urban environment on stress-related brain regions, and in turn potentially act as a preventive measure against developing a mental disorder.

DATA AVAILABILITY

The data supporting the findings of this study are publicly available at https://osf.io/5m2qv/.

CODE AVAILABILITY

The code associated with the data analysis within this study as well as tasks-related code is publicly available at https://osf.io/5m2qv

REFERENCES

1. United Nations, Department of Economic and Social Affairs, Population Division. World Urbanization Prospects: The 2018 Revision (ST/ESA/SER. A/420). New York: United Nations. 2019.
2. Tost H, Champagne FA, Meyer-Lindenberg A. Environmental influence in the brain, human welfare and mental health. Nat Neurosci. 2015;18:1421.
3. Peen J, Dekker J, Schoevers RA, Ten Have M, de Graaf R, Beekman AT. Is the prevalence of psychiatric disorders associated with urbanization? Soc Psychiatry Psychiatr Epidemiol. 2007;42:984–9.
4. Krabbendam L, van Os J. Schizophrenia and urbanicity: a major environmental influence—conditional on genetic risk. Schizophr Bull. 2005;31:795–9.
5. Van Os J. Does the urban environment cause psychosis? Br J Psychiatry. 2004;184:287–8.
6. Lederbogen F, Haddad L, Meyer-Lindenberg A. Urban social stress–risk factor for mental disorders. The case of schizophrenia. Environ Pollut. 2013;183:2–6.
7. Van OsJ, Kenis G, Rutten BP. The environment and schizophrenia. Nature 2010;468:203–12.
8. Berto R. The role of nature in coping with psycho-physiological stress: a literature review on restorativeness. Behav Sci. 2014;4:394–409.
9. Joye Y, van den Berg AE. Restorative environments. In: Steg L, de Groot J, editors. *Environmental psychology: An introduction*. 2nd ed. London: John Wiley & Sons and the British Psychological Society; 2018. p. 65–75.
10. Kellert SR, Wilson EO, The biophilia hypothesis: Island Press; 1993.
11. Wilson EO Biophilia: Harvard University Press; 1984.
12. Kaplan R, Kaplan S The experience of nature: A psychological perspective: Cambridge University Press; 1989.
13. Ulrich RS, Simons RF, Losito BD, Fiorito E, Miles MA, Zelson M. Stress recovery during exposure to natural and urban environments. J Environ Psychol. 1991;11:201–30.
14. Kaplan S. The Restorative Benefits of Nature—toward an Integrative Framework. J Environ Psychol. 1995;15:169–82.
15. Berman MG, Jonides J, Kaplan S. The cognitive benefits of interacting with nature. Psychol Sci. 2008;19:1207–12.
16. Park B-J, Tsunetsugu Y, Kasetani T, Hirano H, Kagawa T, Sato M, et al. Physiological effects of shinrin-yoku (taking in the atmosphere of the forest)—using salivary cortisol and cerebral activity as indicators—. J Physiol Anthropol. 2007;26:123–8.
17. Tost H, Reichert M, Braun U, Reinhard I, Peters R, Lautenbach S, et al. Neural correlates of individual differences in affective benefit of real-life urban green space exposure. Nat Neurosci. 2019;22:1389–93.
18. Oh B, Lee KJ, Zaslawski C, Yeung A, Rosenthal D, Larkey L, et al. Health and well-being benefits of spending time in forests: systematic review. Environ Health Prev Med. 2017;22:71.
19. Park BJ, Tsunetsugu Y, Kasetani T, Kagawa T, Miyazaki Y. The physiological effects of Shinrin-yoku (taking in the forest atmosphere or forest bathing): evidence

from field experiments in 24 forests across Japan. Environ Health Prev Med. 2010;15:18–26.
20. Mao GX, Lan XG, Cao YB, Chen ZM, He ZH, Lv YD, et al. Effects of short-term forest bathing on human health in a broad-leaved evergreen forest in Zhejiang Province, China. Biomed Environ Sci. 2012;25:317–24.
21. Lederbogen F, Kirsch P, Haddad L, Streit F, Tost H, Schuch P, et al. City living and urban upbringing affect neural social stress processing in humans. Nature 2011;474:498–501.
22. Bratman GN, Hamilton JP, Hahn KS, Daily GC, Gross JJ. Nature experience reduces rumination and subgenual prefrontal cortex activation. Proc Natl Acad Sci USA 2015;112:8567–72.
23. Kühn S, Vanderhasselt M-A, De Raedt R, Gallinat J. The neural basis of unwanted thoughts during resting state. Soc Cogn Affect Neurosci. 2013;9:1320–4.
24. Mattavelli G, Sormaz M, Flack T, Asghar AU, Fan S, Frey J, et al. Neural responses to facial expressions support the role of the amygdala in processing threat. Soc Cogn Affect Neurosci. 2014;9:1684–9.
25. Dedovic K, Renwick R, Mahani NK, Engert V, Lupien SJ, Pruessner JC. The Montreal Imaging Stress Task: using functional imaging to investigate the effects of perceiving and processing psychosocial stress in the human brain. J Psychiatry Neurosci. 2005;30:319.
26. Karmanov D, Hamel R. Assessing the restorative potential of contemporary urban environment (s): Beyond the nature versus urban dichotomy. Landsc Urban Plan. 2008;86:115–25.
27. Barnes MR, Donahue ML, Keeler BL, Shorb CM, Mohtadi TZ, Shelby LJ. Characterizing nature and participant experience in studies of nature exposure for positive mental health: An integrative review. Front Psychol. 2019;9:2617.
28. Wager TD, Waugh CE, Lindquist M, Noll DC, Fredrickson BL, Taylor SF. Brain mediators of cardiovascular responses to social threat: Part I: Reciprocal dorsal and ventral sub-regions of the medial prefrontal cortex and heart-rate reactivity. NeuroImage 2009;47:821–35.
29. Kirschbaum C, Pirke K-M, Hellhammer DH. The 'Trier Social Stress Test'–a tool for investigating psychobiological stress responses in a laboratory setting. Neuropsychobiology 1993;28:76–81.
30. Kim MJ, Loucks RA, Neta M, Davis FC, Oler JA, Mazzulla EC, et al. Behind the mask: the influence of mask-type on amygdala response to fearful faces. Soc Cogn Affect Neurosci. 2010;5:363–8.
31. Ohman A, Carlsson K, Lundqvist D, Ingvar M. On the unconscious subcortical origin of human fear. Physiol Behav. 2007;92:180–5.
32. Brooks SJ, Savov V, Allzen E, Benedict C, Fredriksson R, Schioth HB. Exposure to subliminal arousing stimuli induces robust activation in the amygdala, hippocampus, anterior cingulate, insular cortex and primary visual cortex: a systematic meta-analysis of fMRI studies. Neuroimage 2012;59:2962–73.
33. Holland CAC, Ebner NC, Lin T, Samanez-Larkin GR. Emotion identification across adulthood using the Dynamic FACES database of emotional expressions in younger, middle aged, and older adults. Cogn Emot 2019;33:245–57.
34. Gold S, Christian B, Arndt S, Zeien G, Cizadlo T, Johnson DL, et al. Functional MRI statistical software packages: a comparative analysis. Hum Brain Mapp. 1998;6:73–84.
35. Rolls ET, Joliot M, Tzourio-Mazoyer N. Implementation of a new parcellation of the orbitofrontal cortex in the automated anatomical labeling atlas. Neuroimage 2015;122:1–5.
36. Eickhoff SB, Stephan KE, Mohlberg H, Grefkes C, Fink GR, Amunts K, et al. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 2005;25:1325–35.
37. Brett M, Anton J-L, Valabregue R, Poline J-P. Region of interest analysis using an SPM toolbox [abstract]. Presented at the 8th International Conference on Functional Mapping of the Human Brain, June 2-6, 2002, Sendai, Japan. [cited 2021 Nov 20] Available on CD-ROM in NeuroImage, Vol 16, No 2, abstract 497. Available from: http://matthew.dynevor.org/research/abstracts/marsbar/marsbar_abstract.pdf
38. Müller VI, Höhner Y, Eickhoff SB. Influence of task instructions and stimuli on the neural network of face processing: An ALE meta-analysis. Cortex 2018;103:240–55.
39. Johnstone T, Somerville LH, Alexander AL, Oakes TR, Davidson RJ, Kalin NH, et al. Stability of amygdala BOLD response to fearful faces over multiple scan sessions. Neuroimage 2005;25:1112–23.
40. Yang J, Cao Z, Xu X, Chen G. The amygdala is involved in affective priming effect for fearful faces. Brain Cogn. 2012;80:15–22.
41. Jhang J, Lee H, Kang MS, Lee H-S, Park H, Han J-H. Anterior cingulate cortex and its input to the basolateral amygdala control innate fear response. Nat Commun. 2018;9:1–16.
42. Lowry CA, Hale MW Serotonin and the neurobiology of anxious states. Handbook of Behavioral Neuroscience. 21: Elsevier; 2010. p. 379–97.
43. Kühn S, Düzel S, Eibich P, Krekel C, Wüstemann H, Kolbe J, et al. In search of features that constitute an "enriched environment" in humans: Associations between geographical properties and brain structure. Sci Rep. 2017;7:1–8.
44. Wright IC, Rabe-Hesketh S, Woodruff PW, David AS, Murray RM, Bullmore ET. Meta-analysis of regional brain volumes in schizophrenia. Am J Psychiatry. 2000;157:16–25.
45. Van den Berg AE, Ter Heijne M. Fear versus fascination: An exploration of emotional responses to natural threats. J Environ Psychol. 2005;25:261–72.
46. Martens D, Gutscher H, Bauer N. Walking in "wild" and "tended" urban forests: The impact on psychological well-being. J Environ Psychol. 2011;31:36–44.
47. Buijs AE, Elands BH, Langers F. No wilderness for immigrants: Cultural differences in images of nature and landscape preferences. Landsc Urban Plan. 2009;91:113–23.
48. Ordóñez-Barona C. How different ethno-cultural groups value urban forests and its implications for managing urban nature in a multicultural landscape: A systematic review of the literature. Urban Forestry Urban Green. 2017;26:65–77.

ACKNOWLEDGEMENTS

We are grateful for the assistance of the MRI team at the Max Planck for Human Development in Berlin consisting of Sonali Beckmann, Nadine Taube, Thomas Feg, Sebastian Schröder, Nils Bodammer and Davide Santoro and to Maike Hille, Emil Stobbe, Izabela Maria Sztuka, Carlos Raul Cassanello, Mirjam Reidick and Jakob Firnrohr for their help in collecting the data as well as to Nour Tawil for her help in creating the figures.

AUTHOR CONTRIBUTIONS

SS designed and coordinated the study, collected the data, performed neuroimaging data analysis and behavioural data analysis, supported physiological data analysis, and wrote the paper. VS collected the data, supported behavioural data analysis, and analyzed physiological data. SK had the idea for the study, designed and coordinated the study, supervised data acquisition and data analyses, and reviewed the manuscript.

FUNDING

Open Access funding enabled and organized by Projekt DEAL.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41380-022-01720-6.

Correspondence and requests for materials should be addressed to Sonja Sudimac.

Reprints and permission information is available at http://www.nature.com/reprints

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Supplementary information

METHODS

Location of the walks

As recommended in a recent review[1], we report the geographic location of the walks as well as the landscape features. The walk in nature took place in Grunewald forest in Berlin, Germany (Fig. 2b), close to the MRI laboratory (6.7 km, reached within approximately 15 minutes by taxi). The participants walked along Teltower Weg, a path starting at a crossroads between Königsweg and Teltower Weg, spanning towards the north of Grunewald. At over 3000 hectares, Grunewald forest is the largest green area in the city of Berlin. The vegetation of the area is mainly composed of conifers and Betulaceae. Some areas of Grunewald forest are nature reserves and therefore forbidden to visit to protect local fauna, especially amphibians and birds. Apart from the river Havel which forms small islands and a peninsula, Grunewald forest is rich in lakes and ponds, however, the walking route did not pass any water. There are no built structures nor was there any traffic noise during the walking route the participants undertook. Since Grunewald is a recreative forest, it has many paths that people mostly use for walking, jogging, or riding a bicycle.

The urban walk took place in Schloßstraße, a busy street in Berlin-Steglitz (Fig. 2c), close to the MRI laboratory (2.1 km, reachable in approximately 10 minutes by taxi), which consists of two to four traffic lanes. Schloßstraße is one of Berlin's shopping areas, with three shopping malls and three subway stations. Participants were dropped off by the taxi at Schloßstraße 84 and walked northeast, towards Rheinstraße. The participants walked along the sidewalk and could see other people, traffic, buildings, shopping malls, and smaller shops. In Schloßstraße, however, as in most of Berlin's streets, there were also trees, mostly on the sidewalk and on the traffic dividers.

Montreal Imaging Stress Task (MIST)

The Montreal Imaging Stress Task (MIST), a computerized fMRI-adapted task[2], was presented via same projector and mirror system as the FFT and the participants also answered using a response box. In the beginning of the task there was a training session in which the participants' ability to perform mental arithmetic was evaluated, without time limit and a progress bar, to set a default time limit in the Experimental condition.

In the Experimental condition (Suppl. Fig. 1, left), the MIST program reduced the time limit to 10% less than the participant's average time after three correctly solved tasks. When the participants responded incorrectly on three consecutive tasks, the program increased the time limit for the following tasks by 10%. This staircase procedure in the Experimental condition leads to a range of about 20% to 45% of correct answers[2]. In the Experimental condition the information about individual performance and a fake-average performance of all participants was presented after each response with arrows on a performance bar above arithmetic tasks in order to induce social stress. The mathematical arithmetic tasks were designed so that only one digit between 0 and 9 was the correct response. To respond, participants selected a digit on the rotary dial from 0 to 9 by pressing the left or the right button on the button box to highlight the neighboring left or right number until they reached the number they intended to respond with; in that case the middle button was used to confirm the answer. The participant's answer was compared with the correct answer for the arithmetic task and the feedback "Correct" or "Incorrect" was shown in the feedback field. If the time for the arithmetic task ran out, the feedback "Time out" was displayed.

In the Control condition (Suppl. Fig. 1, middle), the mental arithmetic tasks were as difficult as in the Experimental condition. However, the tasks had no time limit and the performance bar comparing the participant's performance and the fake-average performance was not displayed. The feedback for each task was also displayed, but since there was no time limit, average correct performance in the Control condition is around 80% to 90%[2].

Rest condition (Suppl. Fig. 1, right), the participants saw the rotary dial and empty fields for arithmetic tasks and the feedback, but no task was displayed and the participants were asked to simply look at the screen.

The order of the three conditions was randomized within 6 versions of the MIST and the task sequence lasted 14 minutes and 8 seconds. The MIST was retrieved from https://www.millisecond.com, adapted to German language and presented by means of the software Inquisit (version: 5.0.14.0). The code for the MIST together with the stimuli used in this study is openly available at https://osf.io/5m2qv

Social-Evaluative Threat task (SET)

The Social-Evaluative Threat task (SET)[3] is a modified version of the Trier Social Stress Test[4]. While in the MRI scanner, after a baseline phase of two minutes, participants were instructed to prepare for two minutes a 7-minutes speech on the topic "Why am I a good friend?", that they would have to perform in the scanner while being audio- and video-recorded. After the stressor phase, during which fMRI data were acquired, participants were informed that they were randomly selected not to give the speech. The SET task was introduced in order to induce social stress and was presented only at posttest in order to enhance the credibility of the paradigm. At the end of the experiment, during debriefing, participants were informed that no participant had to give the talk. Due to scope of this paper and SET data analysis that differs from the FFT and MIST analysis, the results on the SET task are not reported on here.

Behavioural data

Behavioural measures included questionnaires assessing mood (German version of Positive and Negative Affect Schedule, PANAS[5]), perceived stress during previous hour (adapted German version of Perceived Stress Scale, PSS[6]), rumination during previous hour (adapted Rumination subscale from German version of Rumination Reflection Questionnaire, RRQ[7]), and perceived restorativeness (German version of Perceived Restorativeness Scale, PRS[8]), in addition to a Digit Span Backwards (DSB) task assessing working memory[9]. All behavioural measures were administered at pretest and posttest, except for the PRS which assesses the perceived restorativeness of an environment and was, therefore, reasonable to use only after the walk. Additionally, participants filled out a sociodemographic questionnaire, reported on the weather during the walk as well as the overall pleasantness of the walk, and responded to a German version of the Connectedness to Nature questionnaire[10].

Questionnaires that were administered at pretest and posttest (PANAS, PSS, RRQ) and the DSB task were analyzed using a two-way ANOVA with time as a within-subject factor (before the walk vs. after the walk) and the environment as a between-subject factor (urban vs. natural environment). Due to technical problems, there were missing data for one participant on the DSB task, PANAS, and PSS. Behavioural data from one participant who dropped out at posttest were excluded. As preregistered, participants who scored below or above 2.5 standard deviations from the mean were treated as outliers and excluded from the analyses. Two outliers in the PANAS subscale Negative Affect and in the DSB task were detected and therefore excluded from further analysis. The final sample size for each behavioural measure are reported in the Supplementary Table 8.

PANAS subscale Positive Affect and the RRQ subscale Rumination met the normality assumption and were analyzed using the ezANOVA function from the R package ez[11]. However, since the Shapiro-Wilk normality test indicated that the data were not normally distributed across groups in the PANAS subscale Negative Affect, in the PSS as well as in the DSB, the data for these measures was analyzed with robust ANOVA using the R package WRS2[12]. The Shapiro-Wilk normality test showed that the data normality assumption was not met in the PRS and the question about the pleasantness of the walk, therefore a two-tailed Wilcoxon rank sum test for independent samples was performed, with environment as the independent variable (urban vs. natural environment). The analyses were performed using R software (https://cran.r-project.org/src/base/).

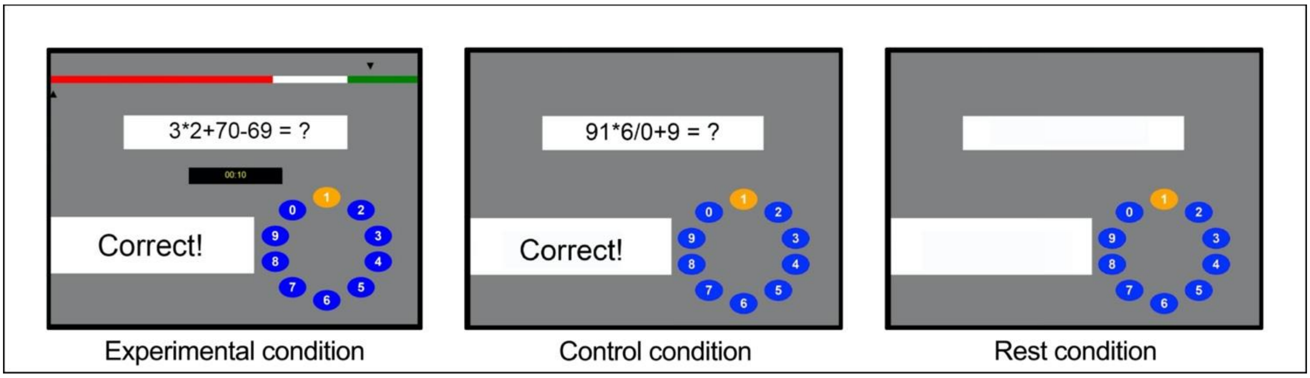
Physiological data

High frequency power band (HF) of heart rate variability (HRV) from the blood volume pulse was selected as a measure of parasympathetic activity[13-16], whereas low frequency divided by high frequency power band (LF/HF) from HRV and heart rate (HR)[13, 14] were used as an index of sympathetic activity[15-21]. LF/HF ratio was computed based on the pre-processed values of LF and HF power band of HRV. HR values were taken directly form the wristband raw data. Electrodermal activity (EDA) signal was decomposed into its phasic and tonic components, and the phasic component was taken as an indicator of sympathetic activity[22, 23]. EDA and blood volume pulse were first preprocessed using the pyPhysio library[24] in Python (https://www.python.org/).

A fixed-length windowing approach was employed[25], resulting in signal indicators' average for each minute. Since the walk lasted up to 60 minutes, the first 54 minutes of the walk were taken into analysis and split into three 18-minute time windows. In order to examine if there was a significant difference in physiological indicators of stress during the walk in the urban vs. natural environment, independent samples t-tests were performed on EDA phasic component, HR, HF power band of HRV and LF/HF ratio of HRV. Physiological indicators of stress were compared between the urban and the natural environment for each of the three 18-minute time windows. Data in time-window 2 and 3 of LF/HF ratio was non-normally distributed, thus a Wilcoxon signed rank test was performed. Since the physiological data of 11 participants were not recorded due to technical difficulties, 52 participants were included in the physiological data analysis. The EDA signal of one participant was too low to be detected after signal processing in Python, resulting in a subsample of 51 participants in the EDA phasic component analysis.

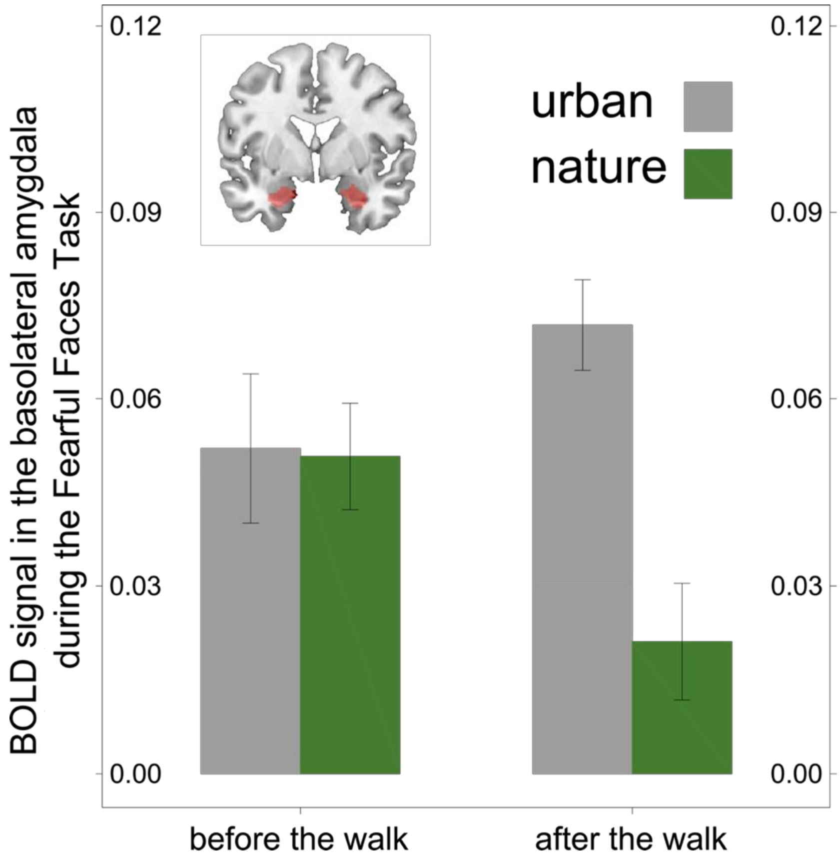
Supplementary Figures

Supplementary Fig. 1: Montreal Imaging Stress Task (MIST) in each of the conditions.



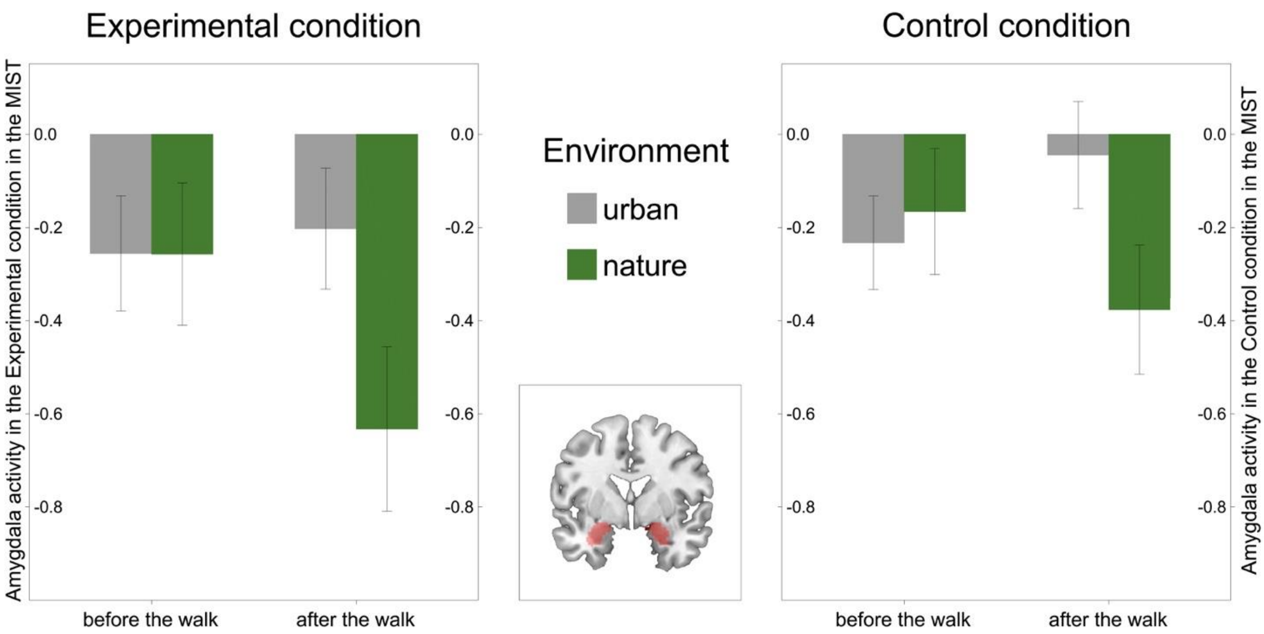
Supplementary Fig.1. Graphical user interface of the Montreal Imaging Stress Task (MIST) in each of the conditions. **Left:** Experimental condition with a bar representing participant's performance (bottom arrow) and fake-average performance (top arrow), the mental arithmetic task, the field showing remaining time for the task, the feedback field and the rotary dial for the response submission; **Middle:** Control condition with the mental arithmetic task, the feedback field and the rotary dial; **Right:** Rest condition with the rotary dial and without mental arithmetic task and feedback.

Supplementary Fig. 2: Basolateral amygdala activity during the Fearful Faces Task before and after the walk in the urban and in the natural environment.



Supplementary Fig. 2. Bilateral basolateral amygdala activity during the Fearful Faces Task (pooled activity during fearful faces and neutral faces) before and after the walk in the urban and in the natural environment. **Top left:** Basolateral amygdala, derived from the SPM Anatomy Toolbox[26].
Note: Error bars represent one standard error of the mean.

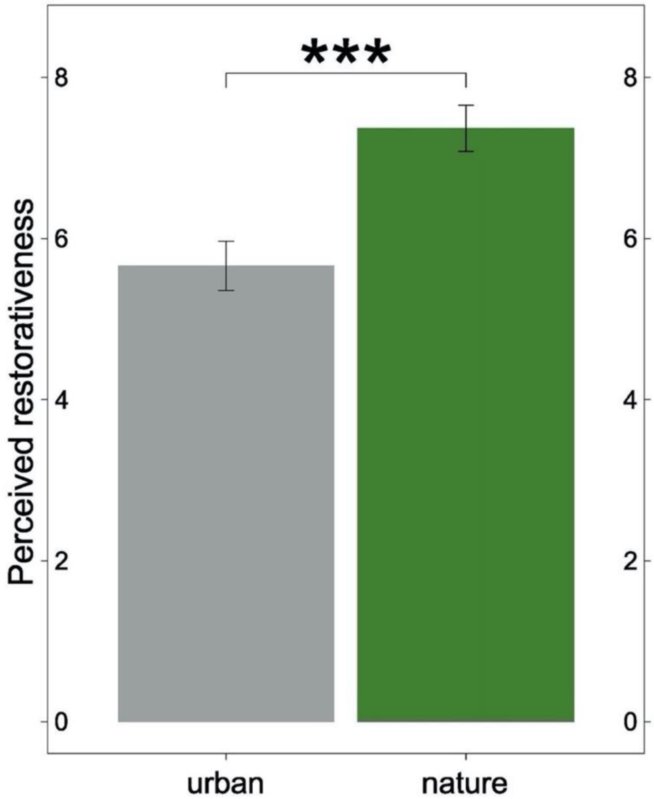
Supplementary Fig. 3: Amygdala activity during the Montreal Imaging Stress Task before and after the walk in the urban and in the natural environment.



Supplementary Fig. 3. Bilateral amygdala activity during Montreal Imaging Stress Task before and after the walk in the urban and in the natural environment. **Left:** Amygdala activity (beta values) in the Experimental condition. **Right:** Amygdala activity (beta values) in the Control condition. **Middle:** Region of interest, the bilateral amygdala activity as defined in Automated Anatomic Labelling Atlas 2.

Note: Error bars represent one standard error of the mean.

Supplementary Fig. 4: Perceived restorativeness of the walk in the urban and in the natural environment.



Supplementary Fig. 4. Score on Perceived Restorativeness Scale after the walk in the urban and in the natural environment.
Note: Error bars represent one standard error from the mean. Significant differences are indicated with asterisks (*** $P < 0.001$).

Supplementary Tables

Supplementary Table 1: Control variables values in the urban and in the natural environment.

Variable	Urban (n = 31)	Nature (n = 32)	$\chi2/t$	*df*	*P* value
Age (mean ± *SD*)	28.58 ± 7.41	25.87 ± 5.52	1.64	55.40	0.107
Sex: female (%)	45	47	0.02	1	0.891
Country of origin: Germany (%)	84	91	0.65	1	0.421
Upbringing: grew up in a city (%)	58	66	0.38	1	0.537
Income: under 1250 euros (%)	71	87.5	2.63	1	0.105
Occupation: students (%)	65	75	0.82	1	0.365
Education: high school diploma (%)	90	91	0.002	1	0.967
Day time: afternoon sessions (%)	45	47	0.02	1	0.891
Air temperature[a] (mean ± *SD*)	16.05 ± 5.12	14.72 ± 5.37	1.00	60.99	0.319
Humidity (%)	68.26 ± 17.82	72.62 ± 19.06	−0.94	60.93	0.351
Cloudiness[b] (mean ± *SD*)	5.71 ± 1.99	6.25 ± 1.85	−1.12	60.35	0.269
Sunny: minutes during 60-minute walk (mean ± *SD*)	30.65 ± 22.62	20.38 ± 22.10	1.82	60.81	0.073
Rainy: walks in the rain (%)	29	31	0.88	1	0.348

Note: Weather values refer to 60 minutes of the walking time; weather data were obtained from the German Meteorological Service (https://www.dwd.de/); *df* = degrees of freedom; *SD* = standard deviation; n = 63

[a]Degrees Celsius (°C)

[b]Amount of cloudiness on an 8-point scale

Supplementary Table 2: Coordinates and anatomical regions significantly activated in the Experimental > Control condition in the Montreal Imaging Stress Task (MIST)

Anatomical region	*t* (peak level)	Voxels	x	y	z
left insula	3.92	129	-15	26	17
right postcentral gyrus	4.37	75	21	-34	62
left superior temporal gyrus	4.01	66	-48	-37	11
left inferior parietal lobule	3.80	40	-39	-25	29

Note: Statistical threshold at $P < 0.001$, uncorrected, while controlling for multiple testing on the cluster level using 3DClutSim within AFNI (Analysis of Functional Neuroimages)[27], k > 34. Anatomical regions were identified using xjView toolbox (https://www.alivelearn.net/xjview).

Descriptive statistics and ANOVA results for brain regions of interest activity in the Fearful Faces Task

Supplementary Table 3: Descriptive statistics and ANOVA results for brain regions of interest activity during fearful faces (Fear condition) in the Fearful Faces Task.

ROI	Mean ± *SD*				*df*	*F*	*P* value	η^2_g
	Urban (n = 31)		Nature (n = 32)					
	pretest	posttest	pretest	posttest				
Bilateral amygdala	0.08 ± 0.08	0.09 ± 0.06	0.08 ± 0.06	0.04 ± 0.08	61	6.11	0.016*	.04
ACC	-0.01 ± 0.06	0.00 ± 0.05	-0.01 ± 0.05	-0.02 ± 0.05	61	1.51	0.224	.01
dlPFC	-0.04 ± 0.05	-0.02 ± 0.04	-0.02 ± 0.05	-0.03 ± 0.04	61	2.16	0.147	.02

Note: Descriptive statistics and a two-way mixed ANOVA interaction effect of factors environment (urban vs. natural) and time (pretest vs. posttest) for each of the region of interest during fearful faces (Fear condition); ROI = region of interest; *SD* = standard deviation; *df* = degrees of freedom; η^2_g= generalized eta-squared effect size; ACC = anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex.
$^*P < 0.05$

Supplementary Table 4: Descriptive statistics and ANOVA results for brain regions of interest activity during neutral faces (Neutral condition) in the Fearful Faces Task.

ROI	Mean ± *SD*				*df*	*F*	*P* value	η^2_g
	Urban (n = 31)		Nature (n = 32)					
	pretest	posttest	pretest	posttest				
Bilateral amygdala	0.07 ± 0.08	0.08 ± 0.06	0.07 ± 0.06	0.03 ± 0.08	61	4.86	0.031*	.03
ACC	-0.01 ± 0.06	-0.01 ± 0.06	0.00 ± 0.06	-0.02 ± 0.06	61	0.81	0.371	.01
dlPFC	-0.03 ± 0.05	-0.02 ± 0.05	-0.02 ± 0.04	-0.03 ± 0.04	61	0.57	0.455	.00

Note: Descriptive statistics and a two-way mixed ANOVA interaction effect of factors environment (urban vs. natural) and time (pretest vs. posttest) for each of the region of interest during neutral faces (Neutral condition); ROI = region of interest; *SD* = standard deviation; *df* = degrees of freedom; η^2_g= generalized eta-squared effect size; ACC = anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex.
*P < 0.05

Supplementary Table 5: Descriptive statistics and ANOVA results for pooled activity of brain regions of interest during fearful and neutral faces (Fear and Neutral condition) in the Fearful Faces Task.

ROI	Mean ± *SD*				*df*	*F*	*P* value	η^2_g
	Urban (n = 31)		Nature (n = 32)					
	pretest	posttest	pretest	posttest				
Bilateral amygdala	0.07 ± 0.08	0.08 ± 0.06	0.08 ± 0.06	0.03 ± 0.08	61	5.81	0.019*	.04
ACC	-0.01 ± 0.06	0.00 ± 0.06	0.00 ± 0.05	-0.02 ± 0.05	61	1.18	0.282	.01
dlPFC	-0.03 ± 0.05	-0.02 ± 0.05	-0.02 ± 0.04	-0.03 ± 0.04	61	1.29	0.261	.01

Note: Descriptive statistics and a two-way mixed ANOVA interaction effect of factors environment (urban vs. natural) and time (pretest vs. posttest) for each of the region of interest during Fearful Faces Task (pooled activity during fearful faces and neutral faces); ROI = region of interest; *SD* = standard deviation; *df* = degrees of freedom; η^2_g= generalized eta-squared effect size; ACC = anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex.
*$P < 0.05$

Descriptive statistics and ANOVA results for brain regions of interest activity in the Montreal Imaging Stress Task (MIST)

Supplementary Table 6: Descriptive statistics and ANOVA results for brain regions of interest activity in the Montreal Imaging Stress Task (MIST).

ROI	Mean ± *SD*				*df*	*F*	*P* value	η^2_g
	Urban (n = 31)		Nature (n = 32)					
	pretest	posttest	pretest	posttest				
Bilateral amygdala	-0.24 ± 0.54	-0.12 ± 0.63	-0.21 ± 0.75	-0.50 ± 0.72	61	5.07	0.028*	.02
ACC	0.00 ± 0.45	0.08 ± 0.63	-0.10 ± 0.56	-0.36 ± 0.74	61	3.16	0.080	.02
dlPFC	-0.01 ± 0.41	0.00 ± 0.48	-0.02 ± 0.40	-0.21 ± 0.49	61	2.16	0.146	.01

Note: Descriptive statistics (pooled activity of Experimental and Control condition) and environment-by-time interaction effect within a 2x2x2 ANOVA of factors environment (urban vs. natural), time (pretest vs. posttest) and condition (Experimental vs. Control) for each of the region of interest in the Montreal Imaging Stress Task; ROI = region of interest; *SD* = standard deviation; *df* = degrees of freedom; η^2_g= generalized eta-squared effect size; ACC = anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex.
$^*P < 0.05$

Supplementary Table 7: Descriptive statistics of behavioural variables.

	Urban		Nature	
Variable	**pretest**	**posttest**	**pretest**	**posttest**
Positive affect[a] (mean ± *SD*)	29.63 ± 5.86	26.80 ± 6.80	27.87 ± 4.53	24.42 ± 8.42
Negative affect[b] (median ± *IQR*)	12.00 ± 4.00	12.00 ± 4.00	12.00 ± 3.00	14.00 ± 7.00
Perceived stress[c] (median ± *IQR*)	16.00 ± 6.50	26.50 ± 8.50	17.00 ± 6.50	27.00 ± 13.00
Rumination[d] (mean ± *SD*)	36.65 ± 8.73	36.65 ± 9.98	42.03 ± 9.62	41.13 ± 9.82
Working memory[e] (median ± *IQR*)	9.00 ± 3.00	9.00 ± 2.50	8.00 ± 2.50	9.00 ± 3.00

Note: SD = standard deviation; *IQR* = interquartile range.

[a]Positive and Negative Affect Schedule (PANAS), subscale Positive Affect. Score ranging from 10 to 50.

[b]Positive and Negative Affect Schedule (PANAS), subscale Negative Affect. Score ranging from 10 to 50.

[c]Perceived Stress Scale. Score ranging from 10 to 50.

[d]Rumination Reflection Questionnaire, subscale Rumination. Score ranging from 12 to 60.

[e]Digit Span Backwards task. Score ranging from 0 to 14.

Supplementary Table 8: ANOVA results of behavioural data.

Variable	***n***	***df***	***F***	***P value***
Positive affect	61	59	0.13	0.719
Negative affect	59	30.47	1.50	0.231
Perceived stress	61	33.93	0.00	0.981
Rumination	62	60	1.42	0.237
Working memory	59	33.90	0.02	0.884

Note: Two-way mixed ANOVA interaction effect of factors environment (urban vs. natural) and time (pretest vs. posttest). The sample size is different because of different number of outliers and data not recorded due to technical problems; *n* = sample size; *df* = degrees of freedom.

Supplementary Table 9: T-test results of physiological indicators of stress.

Variable	Time window	Urban	Nature	*df*	*t*	*P* value
		Mean ± *SD*				
EDA phasic		**(*n* = 26)**	**(*n* = 25)**			
	Time window 1	0.10 ± 0.16	0.10 ± 0.17	47.91	-0.00	0.99
	Time window 2	0.14 ± 0.14	0.15 ± 0.17	45.21	0.12	0.90
	Time window 3	0.29 ± 0.32	0.23 ± 0.21	42.63	-0.84	0.40
HR		**(*n* = 26)**	**(*n* = 26)**			
	Time window 1	69.82 ± 13.03	69.59 ± 16.47	47.48	-0.06	0.95
	Time window 2	79.18 ± 14.35	79.67 ± 20.18	45.14	0.10	0.92
	Time window 3	83.11 ± 14.35	82.98 ± 17.20	48.45	-0.03	0.98
HF power band of HRV		**(*n* = 26)**	**(*n*= 26)**			
	Time window 1	797.68 ± 73.49	794.31 ± 64.81	50.00	-0.18	0.86
	Time window 2	789.13 ± 66.51	799.85 ± 71.66	49.72	0.56	0.58
	Time window 3	785.05 ± 71.37	803.15 ± 92.97	46.87	0.79	0.44
LF/HF of HRV		**(*n* = 26)**	**(*n*= 26)**			
	Time window 1	0.76 ± 0.08	0.74 ±0.09	50.00	-0.56	0.58
		Median ± *IQR*			*z*	***P* value**
	Time window 2	0.71 ± 0.09	0.72 ± 0.08		1.75	0.96
	Time window 3	0.73 ± 0.06	0.74 ± 0.12		0.39	0.65

Note: Results from the t-test analysis examining differences on physiological indicators of stress during the walk in the urban vs. natural environment; Data in time-window 2 and 3 of LF/HF ratio of HRV was non-normally distributed, thus a Wilcoxon signed rank test was performed. *SD* = standard deviation; *IQR* = interquartile range; *n* = sample size; *df* = degrees of freedom. EDA phasic = phasic component of electrodermal activity; HR = heart rate; HF power band of HRV = high frequency power band of heart rate variability; LF/HF of HRV= low frequency power band divided by high frequency power band of heart rate variability.

Supplementary Table 10: Descriptive statistics and results on Perceived restorativeness

	Median ± *IQR*					
	Urban (n = 31)	**Nature (n = 31)**	***n***	***z***	***P* value**	***r***
Perceived restorativeness[a]	5.58 ± 2.21	7.75 ± 1.50	62	−3.85	0.0001***	0.49

Note: Wilcoxon rank sum test examining differences on Perceived restorativeness after the walk in the urban vs. natural environment; Due to non-normal data distribution, Wilcoxon rank sum test was performed; *IQR* = interquartile range; n = sample size; r = effect size (calculated as absolute value of the z score divided by the square root of the sample size).

[a]Perceived restorativeness scale. Scale ranging from 1 to 10.
***$P < 0.001$

REFERENCES

1. Barnes, M.R., *et al.* Characterizing nature and participant experience in studies of nature exposure for positive mental health: An integrative review. *Frontiers in Psychology* **9**, 2617 (2019).
2. Dedovic, K., *et al.* The Montreal Imaging Stress Task: using functional imaging to investigate the effects of perceiving and processing psychosocial stress in the human brain. *Journal of Psychiatry and Neuroscience* **30**, 319 (2005).
3. Wager, T.D., *et al.* Brain mediators of cardiovascular responses to social threat: Part I: Reciprocal dorsal and ventral sub-regions of the medial prefrontal cortex and heart-rate reactivity. *NeuroImage* **47**, 821-835 (2009).
4. Kirschbaum, C., Pirke, K.-M. & Hellhammer, D.H. The 'Trier Social Stress Test'–a tool for investigating psychobiological stress responses in a laboratory setting. *Neuropsychobiology* **28**, 76-81 (1993).
5. Krohne, H., Egloff, B., Kohlmann, C. & Tausch, A. Investigations with a German version of the positive and negative affect schedule (PANAS). *Diagnostica* **42**, 139-156 (1996).
6. Klein, E.M., *et al.* The German version of the Perceived Stress Scale–psychometric characteristics in a representative German community sample. *BMC psychiatry* **16**, 1-10 (2016).
7. Elkhaouda, S. *Geschlechtsspezifische Faktoren in der Vorhersage der Depressivität bei Jugendlichen* (2010).
8. Schönbauer, R. Das Potenzial privater Gärten für die wahrgenommene Gesundheit. (uniwien, 2013).
9. Berman, M.G., Jonides, J. & Kaplan, S. The cognitive benefits of interacting with nature. *Psychol Sci* **19**, 1207-1212 (2008).
10. Cervinka, R., Zeidler, D., Karlegger, A. & Hefler, E. Connectedness with nature, well-being and time spent in nature. in *Program and Abstract of 8th Biennial Conference, Environmental Psychology, September, 6th–9th (S. 130). Lengrich: Pabst Science Publishers* (2009).
11. Lawrence, M.A. & Lawrence, M.M.A. Package 'ez'. *R package version* **4** (2016).
12. Mair, P. & Wilcox, R. Robust statistical methods in R using the WRS2 package. *Behavior research methods* **52**, 464-488 (2020).
13. Jo, H., Song, C. & Miyazaki, Y. Physiological Benefits of Viewing Nature: A Systematic Review of Indoor Experiments. *Int J Environ Res Public Health* **16**, 4739 (2019).
14. Lanki, T., *et al.* Acute effects of visits to urban green environments on cardiovascular physiology in women: A field experiment. *Environ Res* **159**, 176-185 (2017).
15. Lee, J., *et al.* Effect of forest bathing on physiological and psychological responses in young Japanese male subjects. *Public Health* **125**, 93-100 (2011).
16. Shaffer, F., McCraty, R. & Zerr, C.L. A healthy heart is not a metronome: an integrative review of the heart's anatomy and heart rate variability. *Frontiers in psychology* **5**, 1040 (2014).
17. Park, B.J., Tsunetsugu, Y., Kasetani, T., Kagawa, T. & Miyazaki, Y. The physiological effects of Shinrin-yoku (taking in the forest atmosphere or forest bathing): evidence from field experiments in 24 forests across Japan. *Environ Health Prev Med* **15**, 18-26 (2010).
18. Park, B.J., *et al.* Physiological effects of Shinrin-yoku (taking in the atmosphere of the forest) in a mixed forest in Shinano Town, Japan. *Scandinavian Journal of Forest Research* **23**, 278-283 (2008).
19. Ochiai, H., Song, C., Ikei, H., Imai, M. & Miyazaki, Y. Effects of visual stimulation with bonsai trees on adult male patients with spinal cord injury. *International journal of environmental research and public health* **14**, 1017 (2017).
20. Weise, F. & Heydenreich, F. Effects of modified respiratory rhythm on heart rate variability during active orthostatic load. *Biomedica Biochimica Acta* **48**, 549-556 (1989).

21. Goldstein, D.S., Bentho, O., Park, M.Y. & Sharabi, Y. Low-frequency power of heart rate variability is not a measure of cardiac sympathetic tone but may be a measure of modulation of cardiac autonomic outflows by baroreflexes. *Experimental physiology* **96**, 1255-1261 (2011).
22. Benedek, M. & Kaernbach, C. A continuous measure of phasic electrodermal activity. *J Neurosci Methods* **190**, 80-91 (2010).
23. Braithwaite, J.J., Watson, D.G., Jones, R. & Rowe, M. A guide for analysing electrodermal activity (EDA) & skin conductance responses (SCRs) for psychological experiments. *Psychophysiology* **49**, 1017-1034 (2013).
24. Bizzego, A., Battisti, A., Gabrieli, G., Esposito, G. & Furlanello, C. pyphysio: A physiological signal processing library for data science approaches in physiology. *Softwarex* **10**, 100287 (2019).
25. Bizzego, A. A data analytics framework for physiological signals from wearable devices. (University of Trento, 2017).
26. Eickhoff, S.B., *et al.* A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage* **25**, 1325-1335 (2005).
27. Gold, S., *et al.* Functional MRI statistical software packages: a comparative analysis. *Human brain mapping* **6**, 73-84 (1998).

B: Paper II

Sudimac, S., & Kühn, S. (2022). A one-hour walk in nature reduces amygdala activity in women, but not in men. *Frontiers in Psychology*, *13,* 1–13. https://doi.org/10.3389/fpsyg.2022.931905

TYPE Original Research
PUBLISHED 27 September 2022
DOI 10.3389/fpsyg.2022.931905

OPEN ACCESS

EDITED BY
Eugenio De Gregorio,
Università Link Campus,
Italy

REVIEWED BY
Masatoshi Ukezono,
National Center of Neurology and Psychiatry, Japan
Caroll Hermann,
University of Zululand,
South Africa

*CORRESPONDENCE
Sonja Sudimac
sudimac@mpib-berlin.mpg.de

SPECIALTY SECTION
This article was submitted to Environmental Psychology,
a section of the journal
Frontiers in Psychology

RECEIVED 29 April 2022
ACCEPTED 01 September 2022
PUBLISHED 27 September 2022

CITATION
Sudimac S and Kühn S (2022) A one-hour walk in nature reduces amygdala activity in women, but not in men.
Front. Psychol. 13:931905.
doi: 10.3389/fpsyg.2022.931905

A one-hour walk in nature reduces amygdala activity in women, but not in men

Sonja Sudimac[1,2,3]* and Simone Kühn[1,2,4,5]

[1]Lise Meitner Group for Environmental Neuroscience, Max Planck Institute for Human Development, Berlin, Germany, [2]Max Planck Dahlem Campus of Cognition (MPDCC), Max Planck Institute for Human Development, Berlin, Germany, [3]Max Planck Institute for Human Development, International Max Planck Research School on the Life Course (LIFE), Lentzeallee 94, Berlin, Germany, [4]Department of Psychiatry and Psychotherapy, University Medical Center Hamburg-Eppendorf, Hamburg, Germany, [5]Max Planck UCL Centre for Computational Psychiatry and Ageing Research Berlin, Germany and London, UK, Lentzeallee 94, Berlin, Germany

Urban dwellers are more likely to develop mental disorders such as mood and anxiety disorder as well as schizophrenia compared to rural dwellers. Moreover, it has been demonstrated that even short-term exposure to nature can improve mood and decrease stress, but the underlying neural mechanisms are currently under investigation. In the present intervention study we examined the effects of a one-hour walk in an urban vs. natural environment on activity in the amygdala, a brain region previously associated with stress processing. Before and after the walk 63 participants underwent an fMRI paradigm inducing social stress. Since there is a pronounced gap in the literature regarding interindividual differences in stress-related neural effects of urban and natural environments, we set out to explore sex differences. We observed that amygdala activity decreased after the walk in nature, but only in women, suggesting that women may profit more from salutogenic effects of nature. Moreover, performance on the arithmetic tasks improved in women after the walk in nature, whereas men performed better after the walk in the urban environment. To our knowledge, this is the first study to report differencial tendencies in men and women concerning the stress-related neural activity as an effect of acute exposure to urban vs. natural environments. Furthermore, our findings highlight the importance of sex differences when exploring effects of the environment on brain function and stress. Evidence for beneficial effects of nature on stress-related brain regions may inform urban design policies to focus on providing more accessible green areas in cities and this study suggests that sex differences in experiencing the environment should be taken into consideration.

KEYWORDS
environment, nature, urban, sex, brain, amygdala, stress

Introduction

Although living in an urban environment may have benefits, such as accessibility to education, social services, and amenities (Cohen, 2006), it is likewise linked to increased levels of mental disorders such as mood and anxiety disorders, depression and schizophrenia (Peen et al., 2007). Moreover, it has been repeatedly shown that short visits to nature can be beneficial to cognition and mental health. A growing body of empirical research has demonstrated affective (White et al., 2013; Berto, 2014; Barnes et al., 2019) and cognitive benefits of nature exposure (Berman et al., 2008; Ohly et al., 2016; Stevenson et al., 2018).

The pathways and mechanisms by which nature influences psychological well-being are still unclear. The biophilia hypothesis (Wilson, 1984) states that humans feel an innate affection towards all living beings and that this attitude is rooted in our evolutionary past. Based on this account, Attention Restoration Theory (ART) (Kaplan and Kaplan, 1989) proposes that exposure to natural environments restores voluntary attention. Since nature is filled with intrinsically fascinating stimuli (e.g., trees, lakes), it evokes involuntary attention, allowing voluntary attentional processes to recover. Therefore, after exposure to a natural environment, abilities that depend on voluntary attentional mechanisms, such as working memory, should improve (Berman et al., 2008). In accordance with ART, it has been shown that short-term exposure to nature can restore directed attention and improve cognitive capacity (Berman et al., 2008; Ohly et al., 2016; Stevenson et al., 2018). In contrast, Stress Reduction Theory (SRT) (Ulrich et al., 1991) posits that features found in nature such as vegetation, complexity and absence of threat evoke affective responses that lead to restorative processes. In line with SRT, several studies have demonstrated that exposure to natural environments can improve mood (Berman et al., 2008; Hartig et al., 2014; McMahan and Estes, 2015) and have beneficial effects on stress (Oh et al., 2017; Tost et al., 2019). These results are also supported in studies with physiological indicators of stress, showing that heart rate, blood pressure, and cortisol levels decreased after exposure to natural compared to the urban environments (Park et al., 2010; Lee et al., 2011; Mao et al., 2012; Ochiai et al., 2015; Lanki et al., 2017; Ewert and Chang, 2018).

However, the neural mechanisms behind the effects of nature and urban exposure on stress remain largely unstudied. In cross-sectional studies, a positive association was shown between forest coverage around older adults' home and amygdala integrity (Kühn et al., 2017), as well as lower amygdala activity during social stress in rural compared to urban dwellers (Lederbogen et al., 2011), indicating that nature in the neighborhood may have salutogenic effects on the amygdala. On the other hand, research investigating the brain-related effects of short-term exposure to natural vs. urban environment has focused on rumination. A study in which participants went on a 90-min walk in an urban vs. a natural environment showed that self-reported rumination as well as activity in the subgenual prefrontal cortex (sgPFC), associated with rumination, decreased only after the walk in nature, suggesting that exposure to nature may be beneficial in reducing rumination and activity in its neural correlates (Bratman et al., 2015).

To examine the causal effects of acute exposure to natural and urban environments on stress-related neural mechanisms, we conducted a functional magnetic resonance imaging (fMRI) intervention study, measuring a change in stress-related brain regions after a one-hour walk in an urban vs. a natural environment. We observed that during the Fearful Faces Task (FFT), activity in the amygdala, a stress-related brain region, decreased after the walk in nature, whereas it remained stable after the walk in an urban environment, indicating that acute exposure to nature may have salutogenic effects on stress-related brain regions (Sudimac et al., 2022).

Social stress (Lederbogen et al., 2013), experiences due to overcrowding (Kennedy et al., 2009), and lack of green areas in cities (Van den Berg et al., 2010) have been proposed as potential causes of disadvantageous effects of urban environments on mental health. Thus, it has been suggested that spending time in green spaces can attenuate social stress present in urban dwellers (Ulrich et al., 1991). In order to examine the neural mechanism underlying social stress after a walk in a natural vs. urban environment, we employed the Montreal Imaging Stress Task (MIST), a paradigm designed to induce social stress. Comparable to the results of the FFT, a differential effect of environment was observed in the MIST, showing that amygdala activity descriptively decreased during the social stress task only after the walk in nature, suggesting that a one-hour exposure to nature was beneficial for amygdala activity during social stress (Sudimac et al., 2022).

However, little is known about the role of interindividual differences in experiencing urban and natural environments, such as sex. It has been previously shown that women are more connected to nature (Zhang et al., 2014; Dean et al., 2018; Rosa et al., 2020) and appreciate nature's beauty more than men (Zhang et al., 2014). Studies with children have also shown that girls display stronger emotional affinity toward nature than boys (Bagot and Gullone, 2003; Larson et al., 2010). Furthermore, it has been reported that women are more eco-friendly and more concerned about the environment than men (Zelezny et al., 2000). Women consume less carbon and purchase more green products (Zhao et al., 2021) and, as reported in a cross-national study, they show pro-environmental behavior more frequently than men (Hunter et al., 2004). Sex differences were likewise observed in the relation between urban upbringing and brain structure. Namely, gray matter volume in perigenual anterior cingulate cortex (pACC), a key region for regulation of amygdala activity (Pezawas et al., 2005) previously related with urbanicity and stress (Lederbogen et al., 2011), was negatively correlated with years spent in a city during childhood, but only in men (Haddad et al., 2015).

Since sex differences were reported in connectedness to nature (Zhang et al., 2014; Dean et al., 2018; Rosa et al., 2020) and in the association between urban upbringing and gray matter volume (Haddad et al., 2015), in this paper we aimed to explore potential sex differences in amygdala activity change after the walk in the natural vs. urban environment.

Based on the aforementioned literature, we predicted that the walk in nature would have a more beneficial effect for amygdala activity in women compared to men. Furthermore, based on the previous studies showing that exposure to nature is beneficial for attention and cognitive capacity (Berman et al., 2008; Ohly et al., 2016; Stevenson et al., 2018), and taking into account the importance of exploring interindividual differences such as sex when investigating the effects of man-made environments on cognition (Tawil et al., 2021), we predicted that cognitive performance on the MIST would improve after the nature compared to the urban walk and examined potential sex differences.

Materials and methods

Participants

The sample consisted of 63 participants (29 females, total mean age = 27.21 years, *SD* = 6.61, age-range = 18–47 years). The participants were pseudo-randomly assigned either to a nature (32 participants) or an urban walk (31 participants), while controlling for equal distribution of men and women. Participants' age, occupation, education, income and percentage of participants brought up in a city did not significantly differ between the two groups. An overview over the control variables in the two conditions and details about participant recruitment were previously reported elsewhere (Sudimac et al., 2022). Participants were told that they would take part in a magnetic resonance imaging (MRI) study in which they would go for a walk, but were not informed about the research question of the study. All participants were fluent in German, right-handed, and were not diagnosed with any psychological or neurological disorder.

The study was approved by the Local Psychological Ethical Committee at the Center for Psychosocial Medicine at University Medical Center Hamburg-Eppendorf in Hamburg, Germany (LPEK-0054). We obtained written informed consent from all participants and they received monetary compensation.

Study procedure

The experiment was conducted in late summer/fall 2019 between 10:00 a.m. and 5:00 p.m. The flowchart of the study procedure is shown on Figure 1. Upon arrival, participants signed the informed consent, filled out the questionnaires and performed a working memory task. Subsequently, the participants underwent an fMRI scanning procedure that included a resting state sequence with questions on rumination (Kühn et al., 2013), the MIST (Dedovic et al., 2005) and the FFT (Mattavelli et al., 2014). After the scanning session, participants were randomly assigned to a 60-min walk in either a natural (Figure 2, left) or urban environment (Figure 2, right). Even though the definition and also the dichotomy of 'natural' and 'urban' environment has been a subject of debate (Karmanov and Hamel, 2008), the 'natural environment' we refer to is an urban forest, the largest green area in the city of Berlin (Grunewald forest; Figure 2, left), whereas 'urban environment' refers to a busy street in one of the city centers in Berlin with shopping malls (Schloßstraße; Figure 2, right). As recommended in a recent review (Barnes et al., 2019), we previously reported the exact locations of the walk and the characteristics of the urban and natural environments (Sudimac et al., 2022).

The participants were shown the walk on a map (straight path) and subsequently they were picked up at the lab and brought by taxi to the starting point of the walk. They carried a mobile phone that logged their global positioning system (GPS) data during the walk, to ensure that they walked the intended route. Participants went on the walk alone and were instructed not to enter shops or use their mobile phones, to avoid potential distraction. They were given a bagged lunch that they could eat during the walk. After 30 min, an alarm signal went off on the phone, and participants were instructed to turn around and continued the walk back to the starting point. Here they were picked up by a taxi and brought back to the lab.

After the walk the same fMRI scanning procedure was repepated, with one additional stress-inducing task, the Social-Evaluative Threat task (SET; Wager et al., 2009), a modified version of the Trier Social Stress Test (TSST; Kirschbaum et al., 1993), also meant to induce social stress and administered only after the walk at the end of the MRI session, since we reasoned the cover story would not have been credible twice. Finally, participants filled out the questionnaires and were debriefed and informed about the aim of the study.

Functional imaging paradigm

The order of the MIST and the FFT was counterbalanced between participants, but their respective order was the same for each participant at pretest and posttest. The tasks were presented via a projector and mirror system and the participants answered using an MR-compatible response box.

Montreal Imaging Stress Task

The Montreal Imaging Stress Task (MIST; Dedovic et al., 2005) is a computerized fMRI-adapted paradigm, based on the TSST (Kirschbaum et al., 1993) and was administered in order to induce social stress, since the SRT hypothesizes that nature's restorative potential is most evident when the individual is stressed (Ulrich et al., 1991). In the MIST participants solve mental arithmetic tasks with a difficulty and time limit designed to be just beyond participant's cognitive capacities. The MIST consisted of three different conditions: Experimental, Control, and Rest.

In the beginning of the task there was a training session in which the participant's ability to perform mental arithmetic was evaluated, without a time limit or progress bar, to calibrate for a default time limit in the Experimental condition. In the Experimental condition the information about individual performance and a fake-average performance of all participants was presented after each response with arrows on a bar above the arithmetic tasks (Figure 3, above left). This fake-average performance was consistently considerably better than the individual's performance in order to enhance social stress. In the

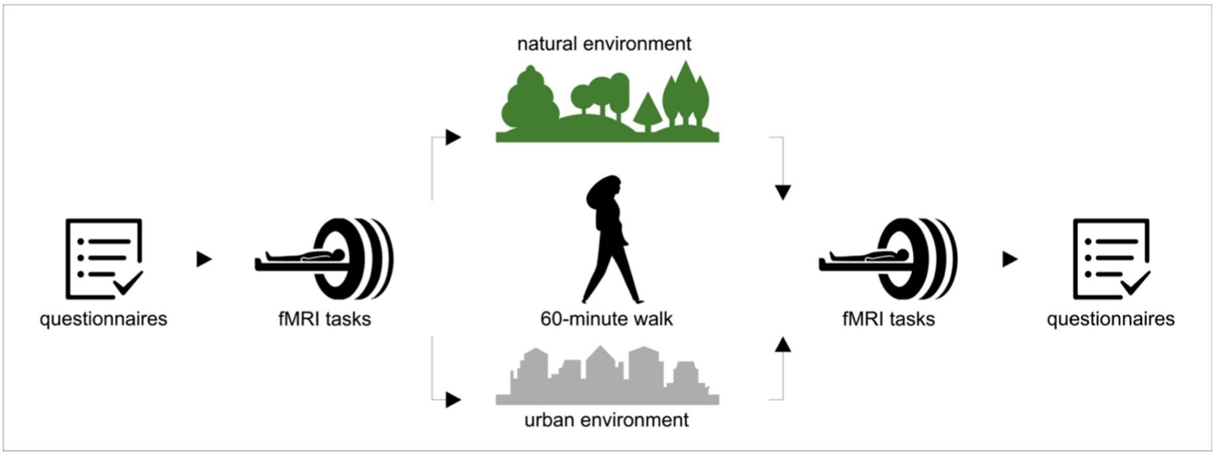


FIGURE 1
Flowchart of the study procedure. Upon arrival participants filled out the questionnaires and then underwent the fMRI scanning procedure, consisting of Montreal Imaging Stress Task (MIST) and Fearful Faces Task (FFT). Subsequently, participants were randomly assigned to go either for a 60-min walk in either a natural or an un urban environment. After the walk participants again underwent the fMRI procedure and at the end they filled out the questionnaires.

FIGURE 2
Location of the nature and urban walk. Left: Sample picture of the route in the natural environment in Grunewald forest, the largest green area in the city of Berlin. Right: Sample picture of the walk in the urban environment Schloßstraße, a busy shopping area with traffic in Berlin.

Experimental condition, the MIST program reduced the time limit to 10% less than the participants's average time after three correctly solved tasks. Conversely, if the participants responded on three consecutive tasks incorrectly, the program increased the time limit for the following tasks by 10%. This staircase procedure in the Experimental condition lead to a range of about 20 to 45% of correct answers (Dedovic et al., 2005). The mathematical arithmetic tasks were designed so that only one digit between 0 and 9 was the correct response. In order to respond, participants selected a digit on the rotary dial from 0 to 9 by pressing the left or the right button on the button box to highlight the neighboring left or right number until they reached the number they intended to respond; in that case the middle button was used to confirm the answer. The participant's answer was compared with the correct answer for the arithmetic task and the feedback "Correct" or "Incorrect" was shown in the feedback field. If the time for the arithmetic task ran out, the feedback "Time out" was displayed (Dedovic et al., 2005).

In the Control condition the mental arithmetic tasks had the same level of difficulty as in the Experimental condition, but the participant's performance as well as the fake-average performance of all participants was not displayed and there was no time limit for solving the task (Figure 3, above right). The feedback for each task was also displayed, but since there was no time limit, average correct performance in the Control condition is around 90% (Dedovic et al., 2005).

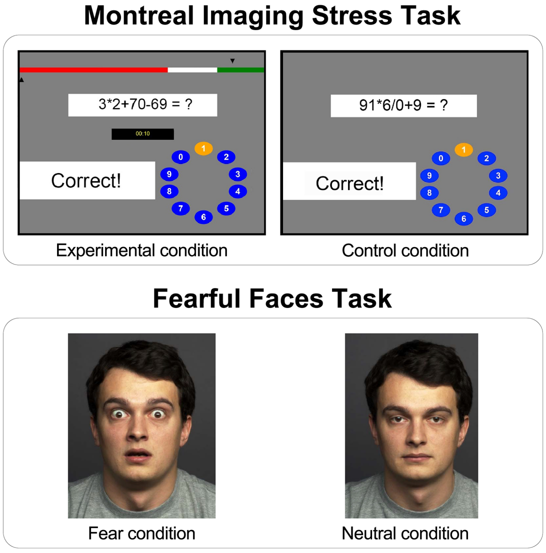


FIGURE 3
Graphical user interface of the Montreal Imaging Stress Task (MIST) and the Fearful Faces Task (FFT). Above left: Experimental condition within the MIST with a bar presenting participant's performance (bottom arrow) and fake-average performance (top arrow), the mental arithmetic task, the field showing remaining time for the task, the feedback field and the rotary dial for the response submission; Above right: Control condition within the MIST with the mental arithmetic task, the feedback field and rotary dial; Below left: Example fearful facial expression stimulus within the FFT (Fear condition); Below right: Example neutral facial expression stimulus within the FFT (Neutral condition).

In the Rest condition, treated as a baseline, the participants saw the rotary dial and empty fields for arithmetic tasks and the feedback, but no task was displayed and the participants were asked to simply look at the screen (Dedovic et al., 2005).

Fearful Faces Task

An adapted version of the Fearful Faces Task (FFT; Mattavelli et al., 2014) was used, designed to measure amygdala activity during fearful and neutral facial expressions. While in the MRI scanner, participants were presented with stimuli consisting of 15 male and 15 female faces, each depicting fearful (Fear condition; Figure 3, below left) or neutral facial expression (Neutral condition; Figure 3, below right). Both fearful and neutral facial expressions were shown either for 1,000 ms (unmasked stimuli) or for 17 ms, followed by a mask with neutral facial expressions presented for 983 ms (masked stimuli), since the amygdala has been shown to respond to masked stimuli even when most of the participants were not aware of their presence (Ohman et al., 2007; Kim et al., 2010; Brooks et al., 2012).

We used the set of 60 stimuli from the FACES database by the Max Planck Institute for Human Development in Berlin (Holland et al., 2019), consisting of face photographs on a gray background, matched on size and luminance. The fMRI paradigm consisted of 22 blocks with 6 pictures interleaved with a 200 ms break between pictures. Each block was followed by a white fixation cross presented for 9 s. In order to monitor the participants' attention, the fixation cross was red on two occasions and participants were instructed to press the button on the response box as soon as they would saw the red cross on the screen. The order of the stimuli was randomized within 10 versions of the FFT, and the task version was introduced in the fMRI data analysis as a covariate. The whole task sequence lasted 8 min and 28 s. The task was presented via a projector and mirror system and the participants answered using the response box. The FFT was presented using the software Presentation (version: 19.0).

Behavioural data

Performance on the Montreal Imaging Stress Task

Performance on the MIST was defined as the percentage of correct answers and mean reaction time (RT) necessary to solve the mental arithmetic tasks in the Experimental condition, during social stress. The percentage of correct answers was analyzed with a two-way ANOVA with environment as a between-subject factor (urban vs. natural) and time as a within-subject factor (before vs. after the walk) using the ezANOVA function from the R package ez (Lawrence and Lawrence, 2016). The same analysis was performed separately within subsamples of women and men. Since the Shapiro–Wilk normality test indicated that female and male subsamples were not normally distributed, we analyzed the percentage of correct answers within each of the subsamples with robust ANOVA using the R package WRS2 (Mair and Wilcox, 2020).

In the RT analysis two participants had a RT that was more than 2.5 SD higher than the mean, therefore they were treated as outliers and excluded from further analysis. The RT was as well analyzed with a two-way ANOVA with environment as a between-subject factor (urban vs. natural) and time as a within-subject factor (before vs. after the walk). Since the RT was not normally distributed across the sample nor across the male subsample, the RT analysis was also performed with robust ANOVA using the R package WRS2 (Mair and Wilcox, 2020). The RT in the female subsample was analyzed with ANOVA using the R package ez (Lawrence and Lawrence, 2016).

Post-hoc t-tests were subsequently conducted for both the percentage of correct answers and the RT in order to examine if there were changes in performance after the walk in the urban and in the natural environment within each of the subsamples.

Questionnaires

Behavioural measures included questionnaires assessing mood [German version of Positive and Negative Affect Schedule, PANAS (Krohne et al., 1996)], perceived stress during the previous hour [adapted German version of Perceived Stress Scale, PSS (Klein et al., 2016)], rumination during the previous hour [adapted Rumination subscale from German version of Rumination Reflection Questionnaire, RRQ (Elkhaouda, 2010)], and perceived restorativeness [German version of Perceived Restorativeness Scale, PRS (Schönbauer, 2013)], in addition to a computerized Digit Span Backwards (DSB) task, which assesses working memory (Berman et al., 2008).

All behavioural measures were administered before and after the walk, except for the PRS which assesses the perceived restorativeness of an environment and was therefore only administered after the walk. Additionally, participants filled out a sociodemographic questionnaire, reported on the weather during the walk and the overall pleasantness of the walk, and responded to a German version of the Connectedness to Nature questionnaire (Cervinka et al., 2009). The results of the analysis of this data as well as of the physiological data (electrodermal activity and heart rate) were previously reported (Sudimac et al., 2022).

Magnetic resonance imaging

Data acquisition

All images were acquired on a Siemens Tim Trio 3 T scanner (Erlangen, Germany) using a 32-channel head coil. The T1-weighted images were obtained using a three-dimensional T1-weighted magnetization prepared gradient-echo sequence (MPRAGE; repetition time (TR) = 2,500 ms; echo time (TE) = 4.77 ms; TI = 1,100 ms, acquisition matrix = 256 × 256 × 192, flip angle = 7°; 1x1x1 mm^3 voxel size). Whole brain functional images were collected using a T2*-weighted echo-planar imaging (EPI) sequence sensitive to BOLD contrast (TR = 2000 ms, TE = 30 ms, acquisition matrix = 216 × 216 × 129, flip angle = 80°, slice thickness = 3.0 mm, distance factor = 20%, FOV = 216 mm, 3 × 3 × 3 mm^3 voxel size, 36 axial slices, using GRAPPA).

Data preprocessing

Functional imaging data were preprocessed and analyzed using Statistical Parametric Mapping software (SPM12[1]). EPIs were corrected for slice timing and head motion and transformed into the stereotactic normalized standard space of the Montreal Neuroimaging Institute (MNI) using the unified segmentation algorithm. Finally, spatial smoothing with a 6-mm full width at half-maximum (FWHM) Gaussian kernel was performed. The voxel size was not changed during preprocessing but kept in the original acquisition dimension (3 × 3 × 3 mm^3).

Data analysis

Montreal Imaging Stress Task

At the first level analysis estimates of functional activation during conditions (Experimental, Control and Rest) were obtained using a blocked analysis. A high-pass filter (cut-off 520 s) was applied. We then used an approach based on our region of interest (ROI), bilateral amygdala. The bilateral amygdala mask was derived from the Automated Anatomic Labelling atlas 2 (Rolls et al., 2015) and had a volume of 3,744 mm^3.

We extracted the beta values for each of the contrasts (Experimental > Rest and Control > Rest) within the bilateral amygdala, using the marsbar toolbox [version 0.44 (Brett et al., 2002)]. As previously reported, we observed a significant interaction in the MIST between environment and time in amygdala pooled activity of the Experimental and Control condition, which descriptively decreased after the walk in nature and remained stable after the walk in the urban environment (Sudimac et al., 2022). In the present study we examined the change in amygdala activity in the MIST in male and female subsample separately. In both subsamples a two-way ANOVA was conducted with environment as a between-subject factor (urban vs. natural) and time as a within-subject factor (before vs. after the walk) in amygdala pooled activity of Experimental and Control condition. Subsequently, two-tailed *post-hoc* *t*-tests were conducted in order to examine if the environment-by-time interaction was driven by a change in amygdala activity after the walk in the urban or in the natural environment.

Fearful Faces Task

At the first level analysis of the FFT, estimates of functional activation during each condition (unmasked Fear, unmasked Neutral, masked Fear, masked Neutral, Response) were modelled using an event-related paradigm. A high-pass filter (cut-off 128 s) was applied and the ROI-based approach was used, focusing on the bilateral amygdala.

We reasoned that the intervention, namely a one-hour walk, would globally affect the stress levels and therewith stress-related brain activity, not only when contrasting the Fear > Neutral condition. Therefore, we examined amygdala activity in the Fear and in the Neutral condition separately, by extracting the blood-oxygen-level dependent (BOLD) signal within the bilateral amygdala using the marsbar toolbox [version 0.44 (Brett et al., 2002)]. We averaged data from unmasked and masked stimuli, because the results were similar.

Within both the male and female subsamples we conducted a two-way ANOVA with environment as a between-subject factor (urban vs. natural) and time as a within-subject factor (before vs. after the walk) in amygdala activity pooled from the Fear and Neutral conditions. Two-tailed *post-hoc* *t*-tests were performed within the urban and the natural environment to examine if the environment-by-time interaction was driven by a change in amygdala activity after the urban walk or the walk in nature.

Results

In the MIST, as hypothesized, we observed a significant environment-by-time interaction in the female subsample in pooled amygdala activity from the Experimental and Control conditions [($F(27) = 4.74$, $p = 0.038$, $\eta^2_g = 0.04$); Figure 4]. The interaction was driven by amygdala activity which descriptively

1 https://www.fil.ion.ucl.ac.uk/spm/software/spm12/

decreased after the walk in nature [$t(14) = 1.89$, $p = 0.080$], whereas it remained stable after the walk in the urban environment [$t(13) = -1.15$, $p = 0.270$; Supplementary Tables 1, 2]. Furthermore, the environment-by-time interaction in the female subsample was driven by a decrease in amygdala activity in the Experimental condition after the walk in nature [($t(14) = 2.35$, $p = 0.034$); Figure 4, left] and by an increase in activation in the Control condition after the walk in the urban environment [($t(13) = -2.62$, $p = 0.021$); Figure 4, right]. In the male subsample, however, there was no significant environment-by-time interaction in amygdala activity [($F(32) = 1.28$, $p = 0.266$, $\eta^2_g = 0.008$); Supplementary Figure 1] and it remained stable after both the walk in the natural [($t(16) = 0.93$, $p = 0.367$)] and the urban environment [($t(16) = -0.66$, $p = 0.516$); Supplementary Tables 1, 2].

In the FFT we observed a significant environment-by-time interaction in the male subsample [$F(32) = 4.37$, $p = 0.045$, $\eta^2_g = 0.05$; Supplementary Figure 2], driven by an increase in amygdala activity after the walk in the urban environment [($t(16) = -1.99$, $p = 0.063$)], while there was no significant interaction in the female subsample [$F(27) = 1.71$, $p = 0.203$, $\eta^2_g = 0.02$]. However, in line with the results on the MIST, amygdala activity after the walk in nature significantly decreased in women [($t(14) = 2.89$, $p = 0.012$); Figure 5], whereas it remained stable in men [($t(16) = 1.06$, $p = 0.303$); Supplementary Tables 1, 2].

Exploratorily, we examined the relationship between the change in amygdala activity after the walk and connectedness to nature score. We observed a positive correlation between the change in amygdala activity on the MIST after the urban walk in women and their connectedness to nature [$r(12) = 0.55$, $p = 0.043$; Supplementary Figure 3], whereas no correlation was found in men [$r(15) = 0.12$, $p = 0.641$].

Regarding the participants' cognitive performance, defined as percentage of correct answers and mean RT in the Experimental condition in the MIST, we observed no significant environment-by-time interaction neither on the whole sample (Supplementary Table 3), nor when splitting the sample into males and females (Supplementary Table 4). Interestingly, the results revealed that men had a higher percentage of correct answers in the Experimental condition in the MIST [$t(54.5) = -2.18$, $p = 0.034$], compared to women.

Post-hoc t-test showed that the percentage of correct answers in the Experimental condition decreased in women after both the urban [$t(13) = 3.03$, $p = 0.010$] and nature walk [$t(14) = 2.68$, $p = 0.019$], as well as in men after the walk in nature [$t(16) = 2.63$,

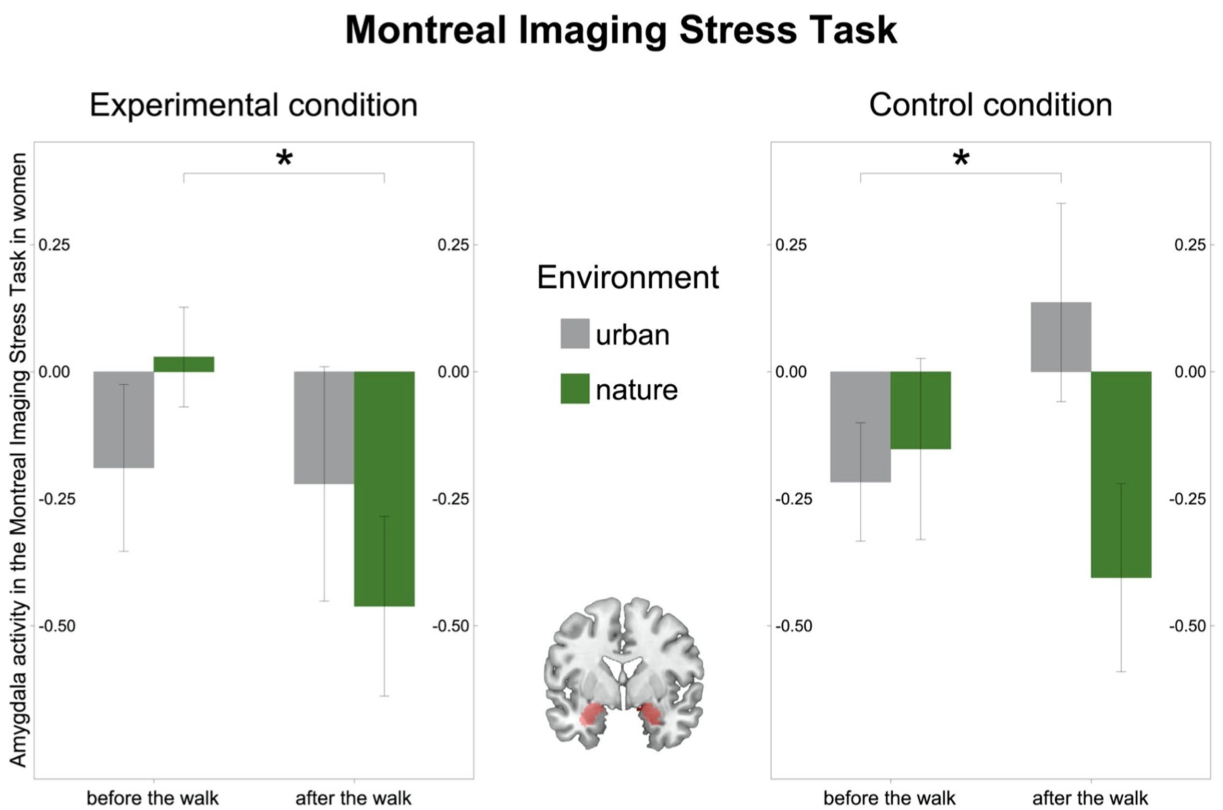


FIGURE 4
Amygdala activity in the Montreal Imaging Stress Task (MIST) in women. Left: Amygdala activity (beta values) in the Experimental condition in the MIST decreased after the walk in the natural environment in women. Right: Amygdala activity (beta values) in the Control condition in the MIST increased after the walk in the urban environment in women. Middle: Region of interest, the bilateral amygdala as defined in Automated Anatomic Labelling Atlas 2. Significant differences are indicated with asterisks (*p<0.05); error bars represent one standard error of the mean.

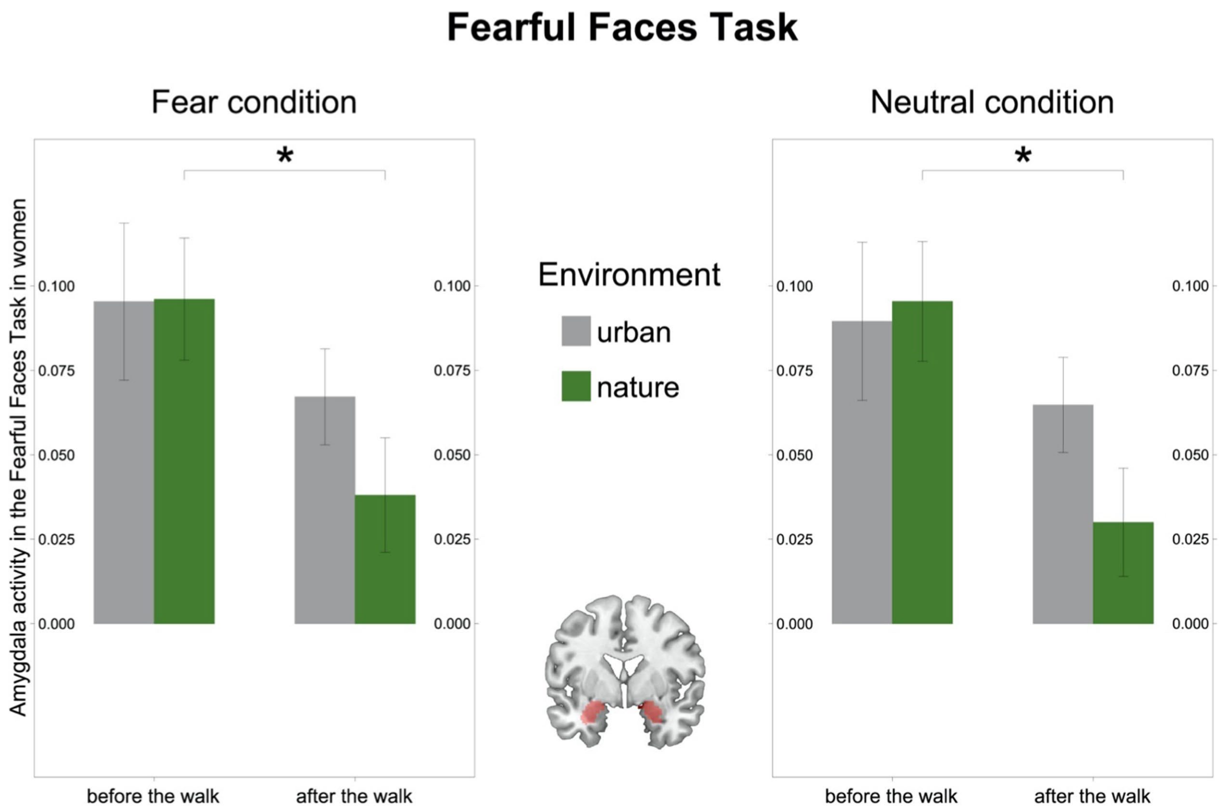


FIGURE 5
Amygdala activity in the Fearful Faces Task (FFT) in women. Left: Amygdala activity (BOLD signal) in the Fear condition in the FFT decreased after the walk in the natural environment in women. Right: Amygdala activity (BOLD signal) in the Neutral condition in the FFT decreased after the walk in the natural environment in women. Middle: Region of interest, the bilateral amygdala as defined in Automated Anatomic Labelling Atlas 2. Significant differences are indicated with asterisks (**p*<0.05); error bars represent one standard error of the mean.

$p = 0.018$], whereas the percentage of correct answers in men did not change after the walk in the urban environment [$t(16) = 1.51$, $p = 0.151$].

However, the mean RT necessary to solve mental arithmetic tasks in the Experimental condition decreased in women only after the walk in nature [$t(13) = 2.60$, $p = 0.022$] and in men only after the walk in the urban environment [$t(16) = 3.14$, $p = 0.006$; Figure 6; Supplementary Table 5]. On the other hand, the RT did not significantly change for women after the walk in the urban environment [$t(13) = 1.96$, $p = 0.072$] nor for men after the walk in the natural environment [$t(15) = 1.76$, $p = 0.099$; Figure 6; Supplementary Table 5].

Discussion

In order to investigate the causal effects of the environment on stress-related brain regions, we conducted an fMRI intervention study in which a change in the amygdala was measured as an effect of a one-hour walk in an urban vs. natural environment. We have previously shown that activity in the amygdala decreased as the result of a one-hour walk in nature, whereas it remained stable after a walk in the urban environment while participants underwent the FFT. Consistent with this finding, a significant environment-by-time interaction during the MIST indicated that amygdala acvitivity descriptively decreased as well on the social stress task after the walk in the natural environment, whereas it remained stable after the walk in the urban environment, suggesting salutogenic effects of nature exposure on the amygdala (Sudimac et al., 2022).

However, there is a pronounced gap in the literature regarding the role of interindividual differences in the effect of exposure to urban and natural environments on brain regions related to social stress. Since sex differences have been previously reported in connectedness to nature (Zhang et al., 2014; Dean et al., 2018; Rosa et al., 2020), as well as in the association between urban upbringing and gray matter volume (Haddad et al., 2015), here we set out to explore sex differences in amygdala activity change as an effect of the urban vs. nature walk.

In line with our hypothesis, in the MIST in the female subsample we observed an interaction between environment and time, showing that amygdala activity during the MIST descriptively decreased after the walk in the natural environment, whereas it remained stable after the walk in the urban environment. On the other hand, the amygdala activity during the MIST in the male subsample did not significantly change after

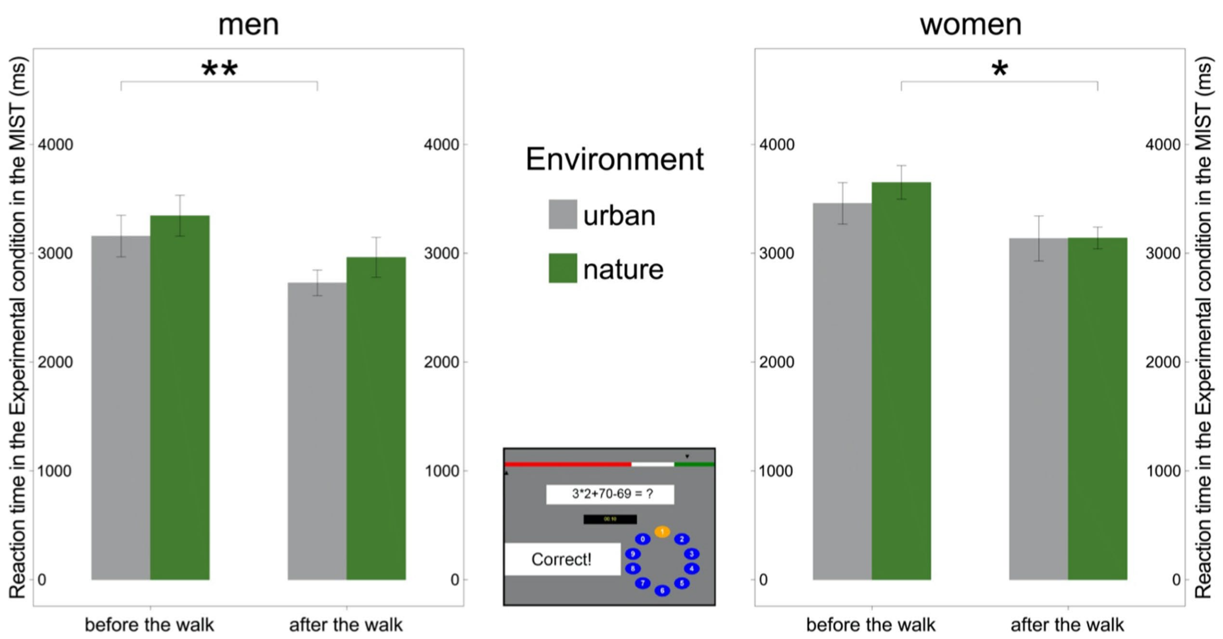


FIGURE 6
Reaction time in the Experimental condition of the Montreal Imaging Stress Task (MIST) by sex. Left: Reaction time in the Experimental condition of the MIST decreased after the walk in the urban environment in men. Right: Reaction time in the Experimental condition in the MIST decreased after the walk in the natural environment in women. Middle: Experimental condition in the MIST. Significant differences are indicated with asterisks (*p<0.05; **p<0.01); error bars represent one standard error of the mean.

both the walk in the urban nor in the natural environment. Similar as in the MIST, within the FFT paradigm we observed a decrease in amygdala activity in women after the walk in nature, whereas it remained stable in men. Therefore, these results altogether suggest that the beneficial effects of nature on stress-related brain regions are more pronounced in women.

Interestingly, in the exploratory analysis we observed that the stronger connectedness to nature was in women, the change in their amygdala activity on the MIST after the city walk was higher, whereas no such association was found in men. Namely, the urban walk increased the stress-related neural activity during the social stress task more in women who are strongly connected to nature, than in those who feel less connected.

Moreover, the reaction time in the mental arithmetic task decreased only in the female subsample after the walk in nature, indicating that the natural environment was also more beneficial to cognition in women than in men. On the other hand, the reaction time decreased only in the male subsample after the urban walk, indicating that the walk in the urban environment was beneficial to cognition in men, but not in women. Interestingly, ART posits that nature restores attention, leading to better cognitive performance after nature exposure (Berto, 2014), however our results suggest that this effect is only observed in women, whereas men benefit cognitively from exposure to an urban environment. However, it should be highlighted that the cognitive performance was measured during the social stress task and therefore it might not be comparable with performance in a common working memory task within the ART approach (Ohly et al., 2016). On the other hand, the results showing a decrease in stress-related neural activity after the walk in nature in women are in accordance with SRT, which predicts that exposure to nature leads to recovery from stress.

To the best of our knowledge this is the first study to demonstrate differential tendencies in amygdala activity change in men and women as a causal effect of acute exposure to a natural vs. urban environment. The findings are in line with results from a pilot study showing that after 20-min exposure to an urban forest (Beil and Hanes, 2013), women reported greater decreases in stress than men. Furthermore, the difference in sex in relatedness to nature was also demonstrated in children, showing that girls reported a more intense positive affect related to natural stimuli (Bagot and Gullone, 2003; Larson et al., 2010), as well as a higher frequency of exposure to natural stimuli, whereas boys reported more intense positive affect related to non-natural stimuli (Bagot and Gullone, 2003). Given that women feel more connected nature (Zhang et al., 2014; Dean et al., 2018; Rosa et al., 2020), appreciate more its beauty more (Zhang et al., 2014) and care about the environment more than men (Zelezny et al., 2000), it might be that nature's relieving effect during social stress is therefore more pronounced in women.

Interestingly, in a previous study in which participants watched 3-D videos with different tree cover density, the relationship between stress recovery and tree densities showed an inverted U-shape in men. Namely, recovery from stress (measured by physiological stress indicators) was positively associated with tree cover density, up to 24%. From 24 to 34% of tree cover density there was no change in stress recovery, whereas higher tree cover density was associated with slower recovery from stress (Jiang et al., 2014). The authors speculate that the slower stress recovery related to high tree density might have been associated with limited sky view and reduction in openness of space, present at higher tree densities. A previous study also reported that natural environments with low openness of space can increase levels of stress (Gatersleben and Andrews, 2013). Since in our study the path where the nature walk took place was mostly surrounded by high coniferous trees, the openness of space was low and the sky view was limited, which, as proposed in the aforementioned study, may have obstructed stress recovery in men after the walk in nature.

To date, few studies have shown that exposure to natural environments had a beneficial effect on cognition in women, whereas the exposure to the urban environment had a beneficial effect on cognition in men. On the other hand, these results are consistent with those of a previous study with children which showed a positive association between nature views from home and benefits in concentration and delayed gratification for girls, but not for boys (Taylor et al., 2002). In correspondence with our finding, it has been shown that stress impairs women's cognitive capacity, whereas it improves cognitive capacity in men (Schoofs et al., 2013) and leads to hyperarousal in women, but not in men (Bangasser et al., 2018). Given that arousal and cognitive performance have an inverted U-shaped relationship, with optimal arousal leading to optimal performance (Fisk et al., 2018), we speculate that the walk in nature decreased high arousal in women, leading to their better cognitive performance. In the same manner, since men under stress are less aroused than women (Bangasser et al., 2018) and stress enhances cognitive capacity in males (Schoofs et al., 2013), the walk in the urban environment, characterized by high social stress, could have increased their arousal and subsequently improved their cognitive performance. However, we have not explicitly tested for self-reported arousal levels after the stress-inducing fMRI paradigm and therefore we have no data on whether arousal levels differ between men and women before the walk. Thus, we recommend that future studies evaluate self-reported stress and arousal after the stress-inducing paradigm before the walk and directly after the walk.

There may also be additional limitations of the present study. The first limitation is a sample bias, since our sample consisted of young adults, mostly students from Germany, a WEIRD (Western, Educated, Industrialized, Rich, Democratic) country. Future studies should include participants from different age ranges, professions and cultures in order to overcome this bias and, especially, to examine the effect of interindividual differences, such as age, culture, personality traits etc. in experiencing urban and natural environments and in their influence on stress-related brain regions. Secondly, even though the MIST has been widely used to induce social stress in neuroimaging studies (Dedovic et al., 2009), social stress is induced by solving arithmetic tasks under time pressure, and therefore level of induced stress may depend on participants' mathematical skills. Considering that during social stress male participants performed better than female participants on the MIST and that a wide range of sociocultural factors contribute to sex differences in interests and achievements in mathematics (Halpern et al., 2007), we recommend that future studies that may choose to focus on sex differences should employ a social stress task that does not rely on participants' previous skills. Thirdly, as discussed in the previous paper (Sudimac et al., 2022), questionnaires given at pretest, before the walk, and at posttest, after the fMRI stress-inducing paradigm, that evaluated the affective state of the participants did not capture the effect of the walk itself, but rather the effect of the stress-inducing paradigm in the scanner and therefore were not used in the analysis with the fMRI data. Finally, it cannot be concluded which features of the nature exposure elicited the decrease in amygdala activity and the reaction time in women, as well as which aspects of the urban environment triggered the decrease in reaction time in men. We would therefore recommend that future studies differentially investigate distinct aspects of natural and urban environments, such as openness of the view, green color, number of people encountered in the environment, noise, odors etc. in order to disentangle specific features of these environments that impact stress-related brain regions.

To summarize, since there is a pronounced gap in the literature regarding interindividual differences in neural effects of exposure to natural vs. urban environments, we examined sex differences. We did so using a social stress paradigm and a fearful faces paradigm focused on activity in the amygdala, a stress-related brain region, as an effect of a one-hour walk in an urban vs. natural environment. We found that amygdala activity decreased after the walk in nature, but only in women, suggesting that women may profit more from the beneficial effects of nature. We also observed that the natural environment improved cognitive performance in women, whereas in men the cognitive performance improved after the walk in the urban environment.

This study is one of the first studies examining stress-related neural effects of an acute exposure to urban vs. natural environments. It is also a seminal study to examine interindividual differences in these effects, such as sex, and to report differential tendencies in men and women regarding their cognitive performance and stress-related neural correlates as a consequence of a short-term exposure to urban vs. natural environments. Therefore, we advise future research not to assume the same salutogenic effects for different population subgroups and to take participants' sex into account, as well as potentially other interindividual differences when investigating the effect of urban and natural environments on cognition, stress and underlying neural mechanisms. The results of this study are significant beacuse they suggest that natural and urban environments may affect men and women differently, which should be taken in account when designing urban green spaces in a way that would be optimal for citizens' mental health.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://osf.io/jazqm/.

Ethics statement

The studies involving human participants were reviewed and approved by Local Psychological Ethical Committee at the Center for Psychosocial Medicine at University Medical Center Hamburg-Eppendorf in Hamburg, Germany. The patients/participants provided their written informed consent to participate in this study.

Author contributions

SS designed and coordinated the study, collected the data, performed data analysis, interpreted the results, and wrote the paper. SK had the idea for the study, designed and coordinated the study, supervised data acquisition and data analyses, interpreted the results, and reviewed the manuscript. All authors contributed to the article and approved the submitted version.

Acknowledgments

We are grateful for the assistance of the MRI team at the Max Planck Institute for Human Development in Berlin consisting of Sonali Beckmann, Nadine Taube, Thomas Feg, Sebastian Schröder, Nils Bodammer, and Davide Santoro and to Maike Hille, Emil Stobbe, Izabela Maria Sztuka, Carlos Raul Cassanello, Vera Sale, Mirjam Reidick, and Jakob Firnrohr for their help in collecting the data as well as to Nour Tawil for her help in creating the figures.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.931905/full#supplementary-material

References

Bagot, K. L., and Gullone, E. (2003). Development and psychometric evaluation of the positive affect schedule for youth (PAS-Y). *Behav. Change* 20, 63–75. doi: 10.1375/bech.20.2.63.24841

Bangasser, D. A., Eck, S. R., Telenson, A. M., and Salvatore, M. (2018). Sex differences in stress regulation of arousal and cognition. *Physiol. Behav.* 187, 42–50. doi: 10.1016/j.physbeh.2017.09.025

Barnes, M. R., Donahue, M. L., Keeler, B. L., Shorb, C. M., Mohtadi, T. Z., and Shelby, L. J. (2019). Characterizing nature and participant experience in studies of nature exposure for positive mental health: an integrative review. *Front. Psychol.* 9:2617. doi: 10.3389/fpsyg.2018.02617

Beil, K., and Hanes, D. (2013). The influence of urban natural and built environments on physiological and psychological measures of stress—a pilot study. *Int. J. Environ. Res. Public Health* 10, 1250–1267. doi: 10.3390/ijerph10041250

Berman, M. G., Jonides, J., and Kaplan, S. (2008). The cognitive benefits of interacting with nature. *Psychol. Sci.* 19, 1207–1212. doi: 10.1111/j.1467-9280.2008.02225.x

Berto, R. (2014). The role of nature in coping with psycho-physiological stress: a literature review on restorativeness. *Behav. Sci.* 4, 394–409. doi: 10.3390/bs4040394

Bratman, G. N., Hamilton, J. P., Hahn, K. S., Daily, G. C., and Gross, J. J. (2015). Nature experience reduces rumination and subgenual prefrontal cortex activation. *Proc. Natl. Acad. Sci. U. S. A.* 112, 8567–8572. doi: 10.1073/pnas.1510459112

Brett, M., Anton, J.-L., Valabregue, R., and Poline, J.-B. (Eds.) (2002). *Region of interest analysis using an SPM toolbox*. 8th International Conference on Functional Mapping of the Human Brain: Sendai.

Brooks, S. J., Savov, V., Allzen, E., Benedict, C., Fredriksson, R., and Schioth, H. B. (2012). Exposure to subliminal arousing stimuli induces robust activation in the amygdala, hippocampus, anterior cingulate, insular cortex and primary visual cortex: a systematic meta-analysis of fMRI studies. *NeuroImage* 59, 2962–2973. doi: 10.1016/j.neuroimage.2011.09.077

Cervinka, R., Zeidler, D., Karlegger, A., and Hefler, E, (Eds.) (2009). *Connectedness with nature, well-being and time spent in nature*. Program and Abstract of 8th Biennial Conference, Environmental Psychology, September, 6th–9th (S130) Pabst Science Publishers Lengrich.

Cohen, B. (2006). Urbanization in developing countries: current trends, future projections, and key challenges for sustainability. *Technol. Soc.* 28, 63–80. doi: 10.1016/j.techsoc.2005.10.005

Dean, J. H., Shanahan, D. F., Bush, R., Gaston, K. J., Lin, B. B., Barber, E., et al. (2018). Is nature relatedness associated with better mental and physical health? *Int. J. Environ. Res. Public Health* 15:1371. doi: 10.3390/ijerph15071371

Dedovic, K., D'Aguiar, C., and Pruessner, J. C. (2009). What stress does to your brain: a review of neuroimaging studies. *Can. J. Psychiatry* 54, 6–15. doi: 10.1177/070674370905400104

Dedovic, K., Renwick, R., Mahani, N. K., Engert, V., Lupien, S. J., and Pruessner, J. C. (2005). The Montreal imaging stress task: using functional imaging to investigate the effects of perceiving and processing psychosocial stress in the human brain. *J. Psychiatry Neurosci.* 30:325.

Elkhaouda, S. (2010). *Geschlechtsspezifische Faktoren in der Vorhersage der Depressivität bei Jugendlichen*.

Ewert, A., and Chang, Y. (2018). Levels of nature and stress response. *Behav. Sci.* 8:49. doi: 10.3390/bs8050049

Fisk, A. S., Tam, S. K., Brown, L. A., Vyazovskiy, V. V., Bannerman, D. M., and Peirson, S. N. (2018). Light and cognition: roles for circadian rhythms, sleep, and arousal. *Front. Neurol.* 9:56. doi: 10.3389/fneur.2018.00056

Gatersleben, B., and Andrews, M. (2013). When walking in nature is not restorative—the role of prospect and refuge. *Health Place* 20, 91–101. doi: 10.1016/j.healthplace.2013.01.001

Haddad, L., Schafer, A., Streit, F., Lederbogen, F., Grimm, O., Wust, S., et al. (2015). Brain structure correlates of urban upbringing, an environmental risk factor for schizophrenia. *Schizophr. Bull.* 41, 115–122. doi: 10.1093/schbul/sbu072

Halpern, D. F., Benbow, C. P., Geary, D. C., Gur, R. C., Hyde, J. S., and Gernsbacher, M. A. (2007). The science of sex differences in science and mathematics. *Psychol. Sci. Public Interest* 8, 1–51. doi: 10.1111/j.1529-1006.2007.00032.x

Hartig, T., Mitchell, R., De Vries, S., and Frumkin, H. (2014). Nature and health. *Annu. Rev. Public Health* 35, 207–228. doi: 10.1146/annurev-publhealth-032013-182443

Holland, C. A. C., Ebner, N. C., Lin, T., and Samanez-Larkin, G. R. (2019). Emotion identification across adulthood using the dynamic FACES database of emotional expressions in younger, middle aged, and older adults. *Cognit. Emot.* 33, 245–257. doi: 10.1080/02699931.2018.1445981

Hunter, L. M., Hatch, A., and Johnson, A. (2004). Cross-national gender variation in environmental behaviors. *Soc. Sci. Q.* 85, 677–694. doi: 10.1111/j.0038-4941.2004.00239.x

Jiang, B., Chang, C.-Y., and Sullivan, W. C. (2014). A dose of nature: tree cover, stress reduction, and gender differences. *Landsc. Urban Plan.* 132, 26–36. doi: 10.1016/j.landurbplan.2014.08.005

Kaplan, R, and Kaplan, S. (1989). *The Experience of Nature: A Psychological Perspective*: Cambridge, MA: Cambridge University Press.

Karmanov, D., and Hamel, R. (2008). Assessing the restorative potential of contemporary urban environment (s): beyond the nature versus urban dichotomy. *Landsc. Urban Plan.* 86, 115–125. doi: 10.1016/j.landurbplan.2008.01.004

Kennedy, D. P., Glascher, J., Tyszka, J. M., and Adolphs, R. (2009). Personal space regulation by the human amygdala. *Nat. Neurosci.* 12, 1226–1227. doi: 10.1038/nn.2381

Kim, M. J., Loucks, R. A., Neta, M., Davis, F. C., Oler, J. A., Mazzulla, E. C., et al. (2010). Behind the mask: the influence of mask-type on amygdala response to fearful faces. *Soc. Cogn. Affect. Neurosci.* 5, 363–368. doi: 10.1093/scan/nsq014

Kirschbaum, C., Pirke, K.-M., and Hellhammer, D. H. (1993). The 'Trier social stress test'–a tool for investigating psychobiological stress responses in a laboratory setting. *Neuropsychobiology* 28, 76–81. doi: 10.1159/000119004

Klein, E. M., Brähler, E., Dreier, M., Reinecke, L., Müller, K. W., Schmutzer, G., et al. (2016). The German version of the perceived stress scale–psychometric characteristics in a representative German community sample. *BMC Psychiatry* 16, 1–10. doi: 10.1186/s12888-016-0875-9

Krohne, H., Egloff, B., Kohlmann, C., and Tausch, A. (1996). Investigations with a German version of the positive and negative affect schedule (PANAS). *Diagnostica* 42, 139–156.

Kühn, S., Düzel, S., Eibich, P., Krekel, C., Wüstemann, H., Kolbe, J., et al. (2017). In search of features that constitute an "enriched environment" in humans: associations between geographical properties and brain structure. *Sci. Rep.* 7, 1–8. doi: 10.1038/s41598-017-12046-7

Kühn, S., Vanderhasselt, M.-A., De Raedt, R., and Gallinat, J. (2013). The neural basis of unwanted thoughts during resting state. *Soc. Cogn. Affect. Neurosci.* 9, 1320–1324. doi: 10.1093/scan/nst117

Lanki, T., Siponen, T., Ojala, A., Korpela, K., Pennanen, A., Tiittanen, P., et al. (2017). Acute effects of visits to urban green environments on cardiovascular physiology in women: a field experiment. *Environ. Res.* 159, 176–185. doi: 10.1016/j.envres.2017.07.039

Larson, L. R., Castleberry, S. B., and Green, G. T. (2010). Effects of an environmental education program on the environmental orientations of children from different gender, age, and ethnic groups. *J. Park Recreation Admin.* 28, 95–113.

Lawrence, MA, and Lawrence, MMA. (2016). Package 'ez'. R package version 4.

Lederbogen, F., Haddad, L., and Meyer-Lindenberg, A. (2013). Urban social stress–risk factor for mental disorders. The case of schizophrenia. *Environ. Pollut.* 183, 2–6. doi: 10.1016/j.envpol.2013.05.046

Lederbogen, F., Kirsch, P., Haddad, L., Streit, F., Tost, H., Schuch, P., et al. (2011). City living and urban upbringing affect neural social stress processing in humans. *Nature* 474, 498–501. doi: 10.1038/nature10190

Lee, J., Park, B. J., Tsunetsugu, Y., Ohira, T., Kagawa, T., and Miyazaki, Y. (2011). Effect of forest bathing on physiological and psychological responses in young Japanese male subjects. *Public Health* 125, 93–100. doi: 10.1016/j.puhe.2010.09.005

Mair, P., and Wilcox, R. (2020). Robust statistical methods in R using the WRS2 package. *Behav. Res. Methods* 52, 464–488. doi: 10.3758/s13428-019-01246-w

Mao, G. X., Lan, X. G., Cao, Y. B., Chen, Z. M., He, Z. H., Lv, Y. D., et al. (2012). Effects of short-term forest bathing on human health in a broad-leaved evergreen forest in Zhejiang Province, China. *Biomed Environ Sci.* 25, 317–324. doi: 10.3967/0895-3988.2012.03.010

Mattavelli, G., Sormaz, M., Flack, T., Asghar, A. U., Fan, S., Frey, J., et al. (2014). Neural responses to facial expressions support the role of the amygdala in processing threat. *Soc. Cogn. Affect. Neurosci.* 9, 1684–1689. doi: 10.1093/scan/nst162

McMahan, E. A., and Estes, D. (2015). The effect of contact with natural environments on positive and negative affect: a meta-analysis. *J. Posit. Psychol.* 10, 507–519. doi: 10.1080/17439760.2014.994224

Ochiai, H., Ikei, H., Song, C., Kobayashi, M., Takamatsu, A., Miura, T., et al. (2015). Physiological and psychological effects of forest therapy on middle-aged males with high-normal blood pressure. *Int. J. Environ. Res. Public Health* 12, 2532–2542. doi: 10.3390/ijerph120302532

Oh, B., Lee, K. J., Zaslawski, C., Yeung, A., Rosenthal, D., Larkey, L., et al. (2017). Health and well-being benefits of spending time in forests: systematic review. *Environ. Health Prev. Med.* 22:71. doi: 10.1186/s12199-017-0677-9

Ohly, H., White, M. P., Wheeler, B. W., Bethel, A., Ukoumunne, O. C., Nikolaou, V., et al. (2016). Attention restoration theory: a systematic review of the attention restoration potential of exposure to natural environments. *J. Toxicol. Environ. Health* 19, 305–343. doi: 10.1080/10937404.2016.1196155

Ohman, A., Carlsson, K., Lundqvist, D., and Ingvar, M. (2007). On the unconscious subcortical origin of human fear. *Physiol. Behav.* 92, 180–185. doi: 10.1016/j.physbeh.2007.05.057

Park, B. J., Tsunetsugu, Y., Kasetani, T., Kagawa, T., and Miyazaki, Y. (2010). The physiological effects of Shinrin-yoku (taking in the forest atmosphere or forest bathing): evidence from field experiments in 24 forests across Japan. *Environ. Health Prev. Med.* 15, 18–26. doi: 10.1007/s12199-009-0086-9

Peen, J., Dekker, J., Schoevers, R. A., Ten Have, M., de Graaf, R., and Beekman, A. T. (2007). Is the prevalence of psychiatric disorders associated with urbanization? *Soc. Psychiatry Psychiatr. Epidemiol.* 42, 984–989. doi: 10.1007/s00127-007-0256-2

Pezawas, L., Meyer-Lindenberg, A., Drabant, E. M., Verchinski, B. A., Munoz, K. E., Kolachana, B. S., et al. (2005). 5-HTTLPR polymorphism impacts human cingulate-amygdala interactions: a genetic susceptibility mechanism for depression. *Nat. Neurosci.* 8, 828–834. doi: 10.1038/nn1463

Rolls, E. T., Joliot, M., and Tzourio-Mazoyer, N. (2015). Implementation of a new parcellation of the orbitofrontal cortex in the automated anatomical labeling atlas. *NeuroImage* 122, 1–5. doi: 10.1016/j.neuroimage.2015.07.075

Rosa, C. D., Larson, L. R., Collado, S., Cloutier, S., and Profice, C. C. (2020). Gender differences in connection to nature, outdoor preferences, and nature-based recreation among college students in Brazil and the United States. *Leis. Sci.* 1-21, 1–21. doi: 10.1080/01490400.2020.1800538

Schönbauer, R. (2013). *Das Potenzial privater Gärten für die wahrgenommene Gesundheit* Vienna uniwien.

Schoofs, D., Pabst, S., Brand, M., and Wolf, O. T. (2013). Working memory is differentially affected by stress in men and women. *Behav. Brain Res.* 241, 144–153. doi: 10.1016/j.bbr.2012.12.004

Stevenson, M. P., Schilhab, T., and Bentsen, P. (2018). Attention restoration theory II: a systematic review to clarify attention processes affected by exposure to natural environments. *J. Toxicol. Environ. Health B Crit. Rev.*, 227–268. doi: 10.1080/10937404.2018.1505571

Sudimac, S., Sale, V., and Kühn, S. (2022). How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in naturez. *Mol. Psychiatry*. doi: 10.1038/s41380-022-01720-6

Tawil, N., Sztuka, I. M., Pohlmann, K., Sudimac, S., and Kühn, S. (2021). The living space: psychological well-being and mental health in response to interiors presented in virtual reality. *Int. J. Environ. Res. Public Health* 18:12510. doi: 10.3390/ijerph182312510

Taylor, A. F., Kuo, F. E., and Sullivan, W. C. (2002). Views of nature and self-discipline: evidence from inner city children. *J. Environ. Psychol.* 22, 49–63. doi: 10.1006/jevp.2001.0241

Tost, H., Reichert, M., Braun, U., Reinhard, I., Peters, R., Lautenbach, S., et al. (2019). Neural correlates of individual differences in affective benefit of real-life urban green space exposure. *Nat. Neurosci.* 22, 1389–1393. doi: 10.1038/s41593-019-0451-y

Ulrich, R. S., Simons, R. F., Losito, B. D., Fiorito, E., Miles, M. A., and Zelson, M. (1991). Stress recovery during exposure to natural and urban environments. *J. Environ. Psychol.* 11, 201–230. doi: 10.1016/S0272-4944(05)80184-7

Van den Berg, A. E., Maas, J., Verheij, R. A., and Groenewegen, P. P. (2010). Green space as a buffer between stressful life events and health. *Soc. Sci. Med.* 70, 1203–1210. doi: 10.1016/j.socscimed.2010.01.002

Wager, T. D., Waugh, C. E., Lindquist, M., Noll, D. C., Fredrickson, B. L., and Taylor, S. F. (2009). Brain mediators of cardiovascular responses to social threat: part I: reciprocal dorsal and ventral sub-regions of the medial prefrontal cortex and heart-rate reactivity. *NeuroImage* 47, 821–835. doi: 10.1016/j.neuroimage.2009.05.043

White, M. P., Alcock, I., Wheeler, B. W., and Depledge, M. H. (2013). Coastal proximity, health and well-being: results from a longitudinal panel survey. *Health Place* 23, 97–103. doi: 10.1016/j.healthplace.2013.05.006

Wilson, E. O. (1984). *Biophilia*. Cambridge, MA: Harvard University Press.

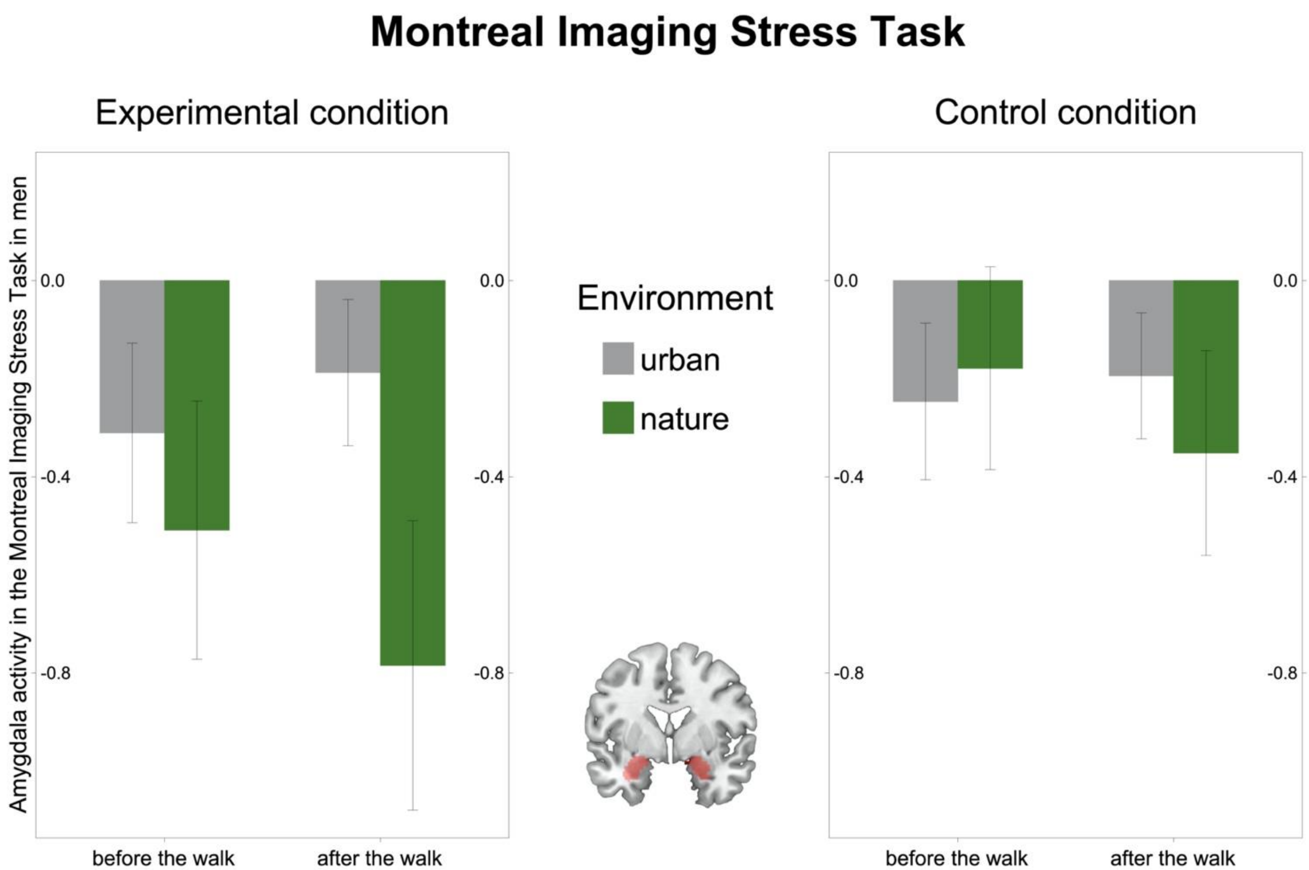
Zelezny, L. C., Chua, P.-P., and Aldrich, C. (2000). Elaborating on gender differences in environmentalism. *J. Soc. Issues* 56, 443–457. doi: 10.1111/0022-4537.00177

Zhang, J. W., Howell, R. T., and Iyer, R. (2014). Engagement with natural beauty moderates the positive relation between connectedness with nature and psychological well-being. *J. Environ. Psychol.* 38, 55–63. doi: 10.1016/j.jenvp.2013.12.013

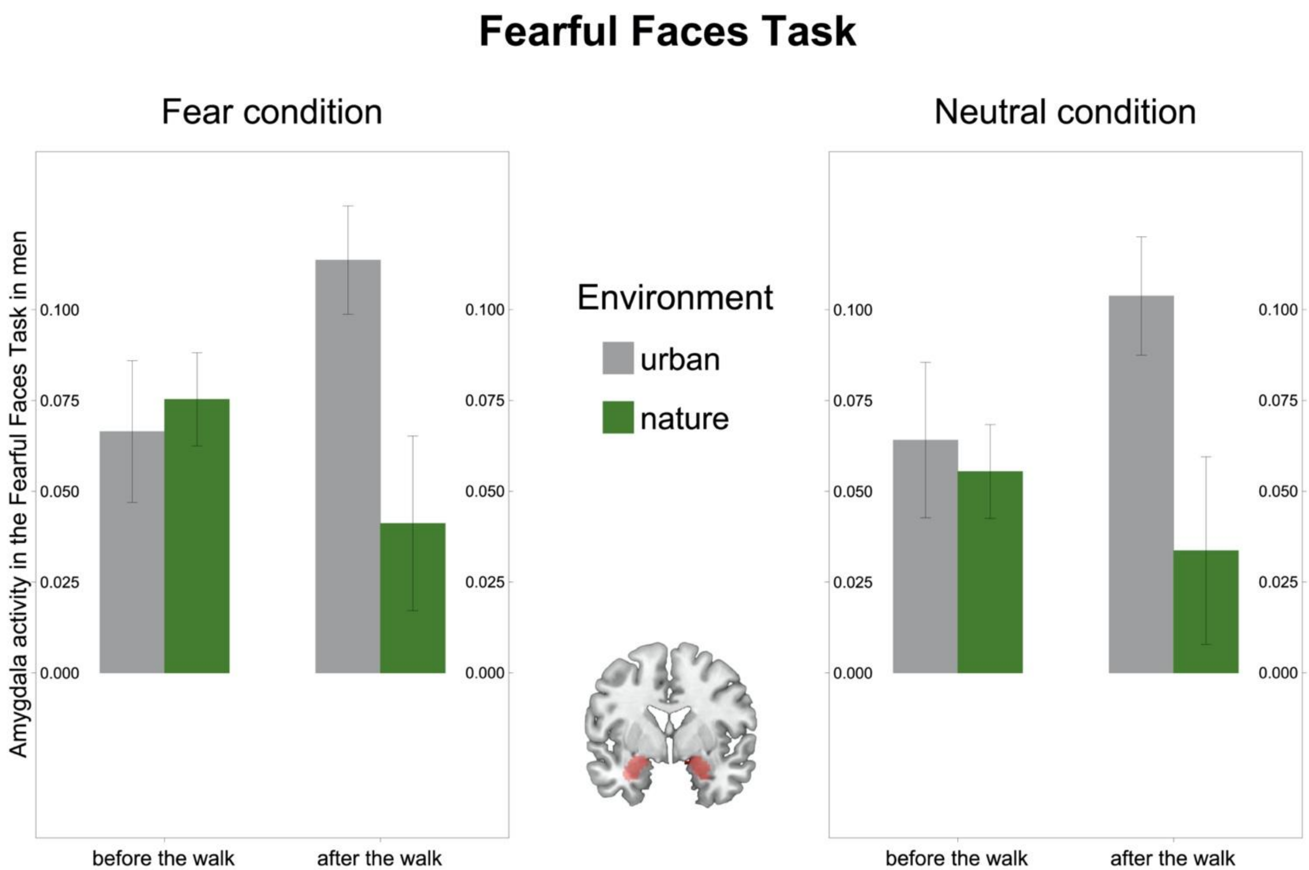
Zhao, Z., Gong, Y., Li, Y., Zhang, L., and Sun, Y. (2021). Gender-related beliefs, norms, and the link with Green consumption, Front. *Psychol.* 12:710239. doi: 10.3389/fpsyg.2021.710239

Supplementary Material

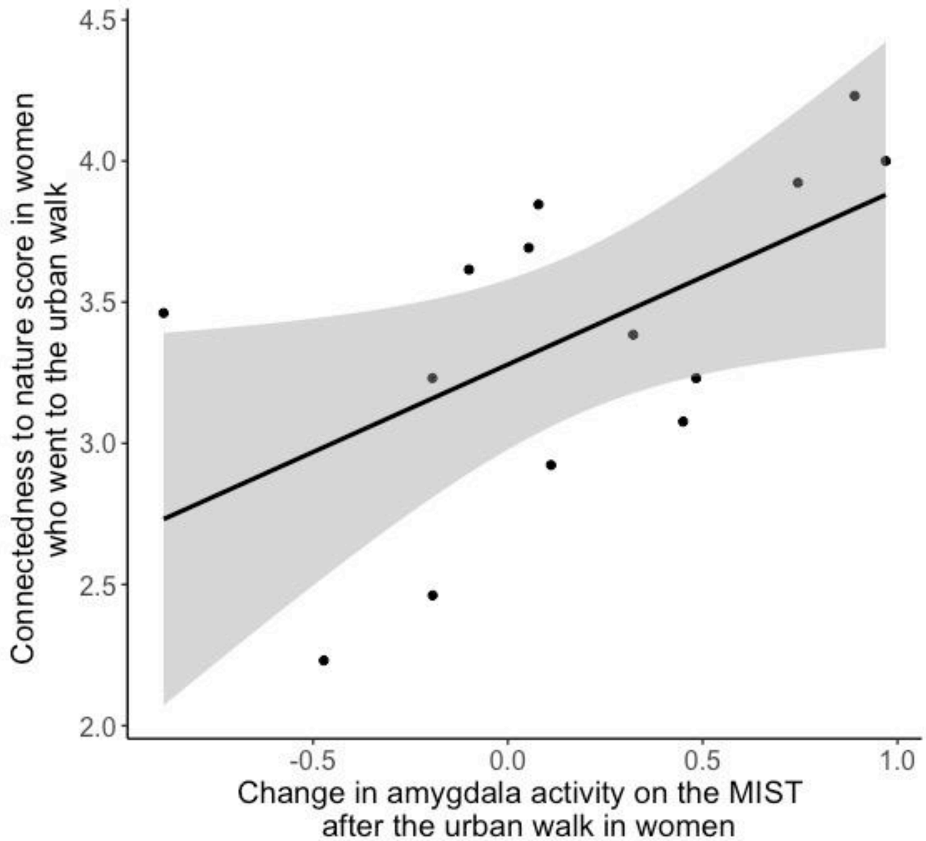
1 Supplementary Figures



Supplementary Figure 1. Amygdala activity in the Experimental and in the Control condition in the Montreal Imaging Stress Task (MIST) in men. Left: Amygdala activity (beta values) in the Experimental condition in the MIST remains stable after the walk in both urban and natural environment in men. **Right:** Amygdala activity in the Control condition in the MIST remains stable after the walk in both urban and natural environment in men. **Middle:** Region of interest, the bilateral amygdala as defined in Automated Anatomic Labelling Atlas 2.



Supplementary Figure 2. Amygdala activity in the Fear and in the Neutral condition in the Fearful Faces Task (FFT) in men. Left: Amygdala activity (BOLD signal) in the Fear condition in the FFT remains stable after the walk in both urban and natural environment in men. **Right:** Amygdala activity (BOLD signal) in the Neutral condition in the FFT remains stable after the walk in both urban and natural environment in men. **Middle:** Region of interest, the bilateral amygdala as defined in Automated Anatomic Labelling Atlas 2.



Supplementary Figure 3. Relationship between a change in amygdala activity on the Montreal Imaging Stress Task (MIST) after the urban walk in women and their connectedness to nature.

2 Supplementary Tables

Supplementary Table 1: Post hoc t-test between pretest and posttest for bilateral amygdala activity in the Fearful Faces Task (FFT) and in the Montreal Imaging Stress Task (MIST) by sex.

	Men						Women					
	Urban (*n* = 17)			Nature (*n* = 17)			Urban (*n* = 14)			Nature (*n* = 15)		
Task	**t-test**	***df***	***P value***	**t-test**	***df***	***P* value**	**t-test**	***df***	***P value***	**t-test**	***df***	***P* value**
FFT	-1.99	16	0.063	1.06	16	0.303	1.65	13	0.122	2.89	14	0.012*
MIST	-0.66	16	0.516	0.93	16	0.367	-1.15	13	0.270	1.89	14	0.080

Note: Post-hoc t-tests (pretest vs. posttest) for bilateral amygdala activity in the Fearful Faces Task (pooled activity during Fear and Neutral condition) and in the Montreal Imaging Stress Task (pooled activity during Experimental and Control condition) by sex; *df* = degrees of freedom; *$P < 0.05$, refers to BOLD activity/beta values.

Supplementary Table 2: Descriptive statistics for bilateral amygdala activity in the Fearful Faces Task (FFT) and in the Montreal Imaging Stress Task (MIST) by sex.

	Mean ± *SD*							
	Men				Women			
	Urban (*n* = 17)		Nature (*n* = 17)		Urban (*n* = 14)		Nature (*n* = 15)	
Task	**pretest**	**posttest**	**pretest**	**posttest**	**pretest**	**posttest**	**pretest**	**posttest**
FFT	0.06±0.07	0.10±0.06	0.06±0.05	0.03±0.09	0.09±0.09	0.07±0.05	0.10±0.07	0.03±0.06
MIST	-0.28±0.61	-0.19±0.52	-0.34±0.91	-0.57±0.81	-0.20±0.46	-0.04±0.75	-0.06±0.50	-0.43±0.63

Note: Descriptive statistics for bilateral amygdala activity in the Fearful Faces Task (pooled activity during Fear and Neutral condition) and in the Montreal Imaging Stress Task (pooled activity during Experimental and Control condition) by sex; *SD* = standard deviation, refers to BOLD activity/beta values.

Supplementary Table 3: ANOVA results of the cognitive performance in the Experimental condition of the Montreal Imaging Stress Task (MIST)

Cognitive performance indicator	***df***	***F***	***P value***
Percentage of correct answers	61	0.05	0.831
Reaction time	35.98	0.38	0.541

Note: Two-way mixed ANOVA interaction effect of factors environment (urban vs. natural) and time (pretest vs. posttest) on percentage of correct answers and reaction time in the Experimental condition of the Montreal Imaging Stress Task (MIST); Due to non-normal distribution, analysis of the Reaction time was performed using robust ANOVA; *df* = degrees of freedom.

Supplementary Table 4: ANOVA results of the cognitive performance in the Experimental condition of the Montreal Imaging Stress Task (MIST) by sex

	Men				Women			
Cognitive performance indicator	*df*	*F*	*P value*	η^2_g	*df*	*F*	*P value*	η^2_g
Percentage of correct answers	16.56	1.94	0.182	0.02	16.48	1.87	0.190	0.007
Reaction time	19.07	0.48	0.497	0.0002	26	0.50	0.484	0.006

Note: Two-way mixed ANOVA interaction effect of factors environment (urban vs. natural) and time (pretest vs. posttest) on percentage of correct answers and reaction time in the Experimental condition of the Montreal Imaging Stress Task (MIST) by sex; Due to non-normal distribution, analysis of the variables Percentage of correct answers in male and female subsamples and the Reaction time in the male subsample was performed using robust ANOVA; *df* = degrees of freedom. η^2_g= generalized eta-squared effect size.

Supplementary Table 5: Descriptive statistics for mean reaction time for solving mental arithmetic tasks in the Experimental condition in the Montreal Imaging Stress Task (MIST) by sex

Mean ± *SD*							
Men				Women			
Urban (*n* = 17)		Nature (*n* = 16)		Urban (*n* = 14)		Nature (*n* = 14)	
pretest	posttest	pretest	posttest	pretest	posttest	pretest	posttest
3154 ± 788	2728 ± 482	3342 ± 750	2959 ± 736	3459 ± 724	3131 ± 767	3650 ± 587	3139 ± 376

Note: Descriptive statistics for mean reaction time (in milliseconds) for solving mental arithmetic tasks in the Experimental condition of the Montreal Imaging Stress Task (MIST) by sex and condition; Scores of two participants were excluded from the analysis as outliers; *SD* = standard deviation.

C: Paper III

Sudimac, S., & Kühn, S. (2024). *Can a nature walk change your brain? Investigating hippocampal brain plasticity after one hour in a forest.* PsyArXiv. https://doi.org/10.31234/osf.io/g64bq [Manuscript under revision]

Can a nature walk change your brain? Investigating hippocampal brain plasticity after one hour in a forest

Sonja Sudimac[1] & Simone Kühn[1,2,3]

Affiliations:

[1] Max Planck Institute for Human Development,
Lise Meitner Group for Environmental Neuroscience,
Lentzeallee 94, 14195 Berlin, Germany

[2] University Medical Center Hamburg-Eppendorf,
Department of Psychiatry and Psychotherapy,
Martinistr. 52, 20251 Hamburg, Germany

[3] Max Planck UCL Centre for Computational Psychiatry
and Ageing Research Berlin, Germany and London, UK,
Lentzeallee 94, 14195 Berlin Germany

Corresponding author: Sonja Sudimac
e-mail: sudimac@mpib-berlin.mpg.de

Abstract

Incidence of mental disorders is higher in cities, whereas visits to nature have been reported to be beneficial for mental health and brain function. However, there is a lack of knowledge regarding how exposure to natural and urban environments affects brain structure. To examine the causal relationship between exposure to these environments and hippocampal formation, 60 participants were subjected to a one-hour walk in either natural (forest) or urban environment (busy street), and high-resolution hippocampal imaging was performed before and after the walks. We observed that the participants who walked in the forest showed increases in subiculum volume, a hippocampal subfield involved in stress response inhibition, while no change was observed after the urban walk. However, this result did not withstand Bonferroni correction for multiple comparisons. Furthermore, the increase in subiculum volume after the forest walk was associated with a decrease in self-reported rumination. These results indicate that visits to nature can lead to observable alterations in the brain structure, with potential benefits for mental health and implications for public health and urban planning policies.

1. Introduction

It has been repeatedly shown that mental health problems, such as anxiety disorders, schizophrenia, and depression are more common in cities [1], [2]. Moreover, a growing body of research shows that going to nature enhances mental health [3], [4], [5]. Even brief exposures to natural environments have a positive impact on mood by increasing positive affect and decreasing negative affect [6]. Negative affect, in particular depressivity is related to rumination [7], [8] − a maladaptive pattern of repetitive negative self-referential thinking, that can predict onset of depression[8].

It has been shown that a 90-min [9] or even 30-min [10] nature walk decreases rumination. However, only few studies have examined the neural mechanisms underlying these beneficial effects of nature on rumination and mental health. In a seminal study it was demonstrated that a walk in nature reduced both rumination and activity in the subgenual prefrontal cortex, a brain region linked to self-referential thoughts [9]. We have recently shown that a one-hour walk in a forest decreased activity in the amygdala, a brain region associated with stress processing, likewise suggesting that nature has salutogenic effects on brain health[11]. Although these studies provide insights on how exposure to natural and urban environments affects brain function, little is known about the effects on brain structure.

Several recent studies have shown that living close to natural environments is positively associated with brain structural health metrics, such as cortical thickness and grey matter volume [12], [13]. Thus, a cross-sectional study examining differences in brain structure associated with the environment during ontogenetic upbringing showed that hippocampal and parahippocampal formation was larger in adolescents who were raised exclusively in rural areas than in those who were exclusively raised in cities [14]. Nevertheless, in order to examine the causal relationship between exposure to urban vs. natural environments and brain structure, intervention studies are required. To the best of our knowledge, changes in brain structure after short-term exposure to natural and urban environments have not to date been investigated.

Even though it is generally assumed that brain structure is relatively stable, several studies have shown rapid changes in structural magnetic resonance imaging (MRI) markers. Namely, spending more time outdoors 24 hours before scanning seems to have a substantial impact on grey matter volume in the dorsolateral prefrontal cortex [15]. Furthermore, microstructural changes in the hippocampus and parahippocampus were detected already after two hours of performing a spatial learning task [16].

Since the hippocampal formation has previously been associated with the physical environment during upbringing [14] and is known for its potential to display rapid structural reorganization [16], we set out to explore how a one-hour exposure to an urban vs. natural environment may impact hippocampal structure. Additionally, as a walk in nature decreases rumination [9], [10], and ruminative thoughts have been associated with the hippocampus [17], [18], [19] we set out to examine the association between potential change in hippocampal structure and a change in rumination elicited by the walk.

2. Results

In order to examine how exposure to natural vs. urban environments affects hippocampal formation, we conducted an MRI intervention study (Figure 1). High-resolution hippocampal imaging was performed before and after a one-hour walk in a natural environment (urban forest Grunewald; Figure 2b) vs. urban environment (busy street in Berlin; Figure 2c).

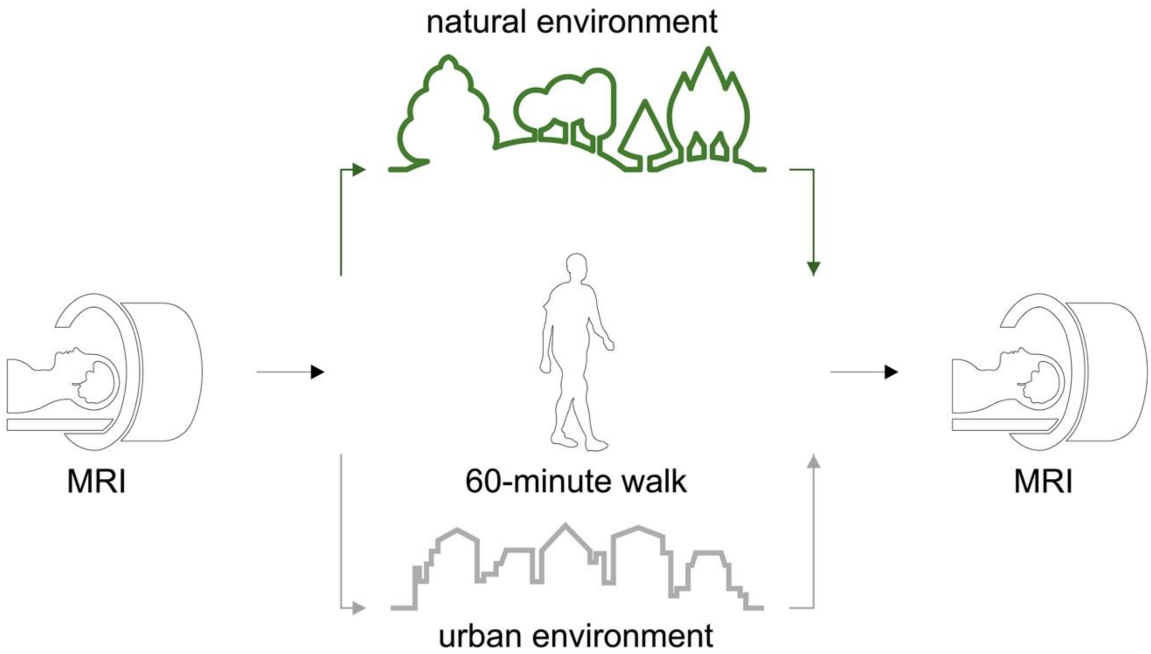


Figure 1. Flowchart of the study procedure. Before the walk participants underwent the MRI scanning procedure. Subsequently, each participant was randomly assigned to a 60-min walk, in either a natural or urban environment. After the walk, the participants underwent the MRI scanning procedure again. Adapted from "How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature" by Sudimac et al., 2022, *Molecular Psychiatry, 27*, p. 4448

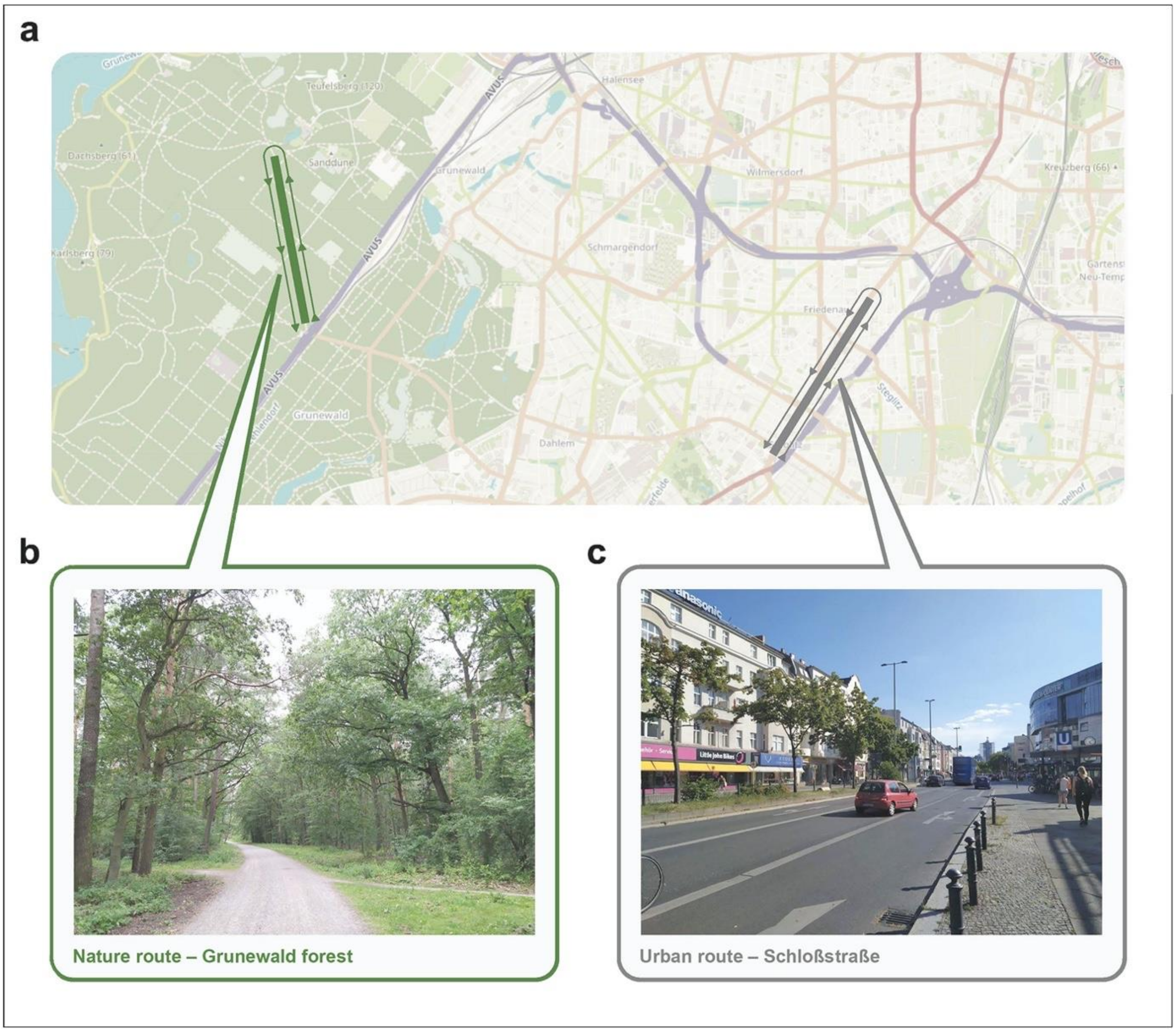


Figure 2. Location of the nature and urban walk. a GPS data of two participants during the walk in the natural environment (Berlin, Grunewald) and the urban environment (Berlin, Schloßstraße) displayed on the OpenStreetMap (https://www.openstreetmap.org). **b** Sample picture of the walk in the natural environment. **c** Sample picture of the walk in the urban environment. Reprinted from "How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature" by Sudimac et al., 2022, *Molecular Psychiatry, 27*, p. 4448

A significant environment-by-time interaction was observed in bilateral subiculum volume ($F(1,58) = 4.717$, $p = 0.034$, $\eta^2_g = 0.01$; Figure 3), which increased after the walk in nature ($t(29) = -2.758$, $p = 0.010$; see Supplementary Table S1 online), but not after the urban walk ($t(29) = -0.133$, $p = 0.895$). The volumes of the other hippocampal subfields, as well as those of the amygdala and the hippocampus, showed no significant interaction effects. However, the significant interaction does not survive conservative Bonferroni multiple comparison correction. Post-hoc we explored potential lateralization effects and observed that the effect was mostly driven by the right, not the left subiculum (right: $F(1,58) = 5.626$, $p = 0.021$, $\eta^2_g = 0.01$; left: $F(1,58) = 2.259$, $p = 0.138$, $\eta^2_g = 0.01$).

We then associated the change in subiculum volume, the only hippocampal subfield where environment-by-time interaction was observed, with the change in rumination score separately for the nature and the urban condition. Changes in bilateral subiculum were negatively associated with changes in rumination in the nature ($r(28) = -0.367$, $p = 0.046$; Figure 4), but not in the urban environment ($r(28) = 0.102$, $p = 0.592$), with the difference of correlation coefficients being significant (Fisher's $z = 1.79$, $p = 0.037$). There was no environment-by-time interaction for self-reported rumination.

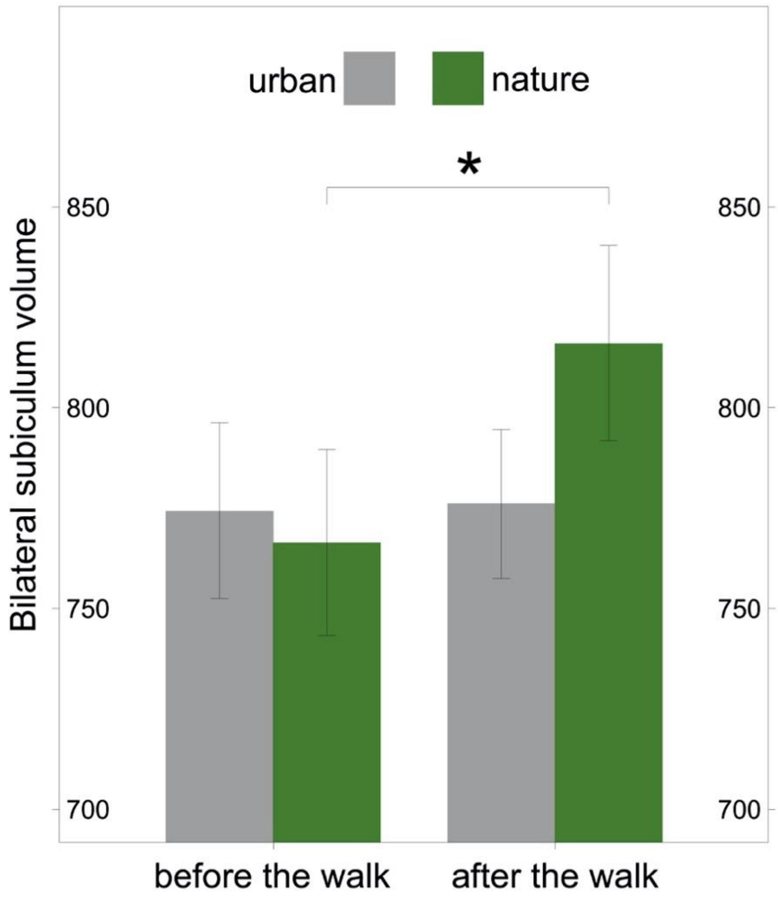


Figure 3. Bilateral subiculum volume before and after the walk in the urban and in the natural environment. Bilateral subiculum volume increased after the walk in the forest, whereas it did not change after the walk in the urban environment. *Note:* Significant differences are indicated with asterisk (*$p < 0.05$); error bars represent one standard error of the mean.

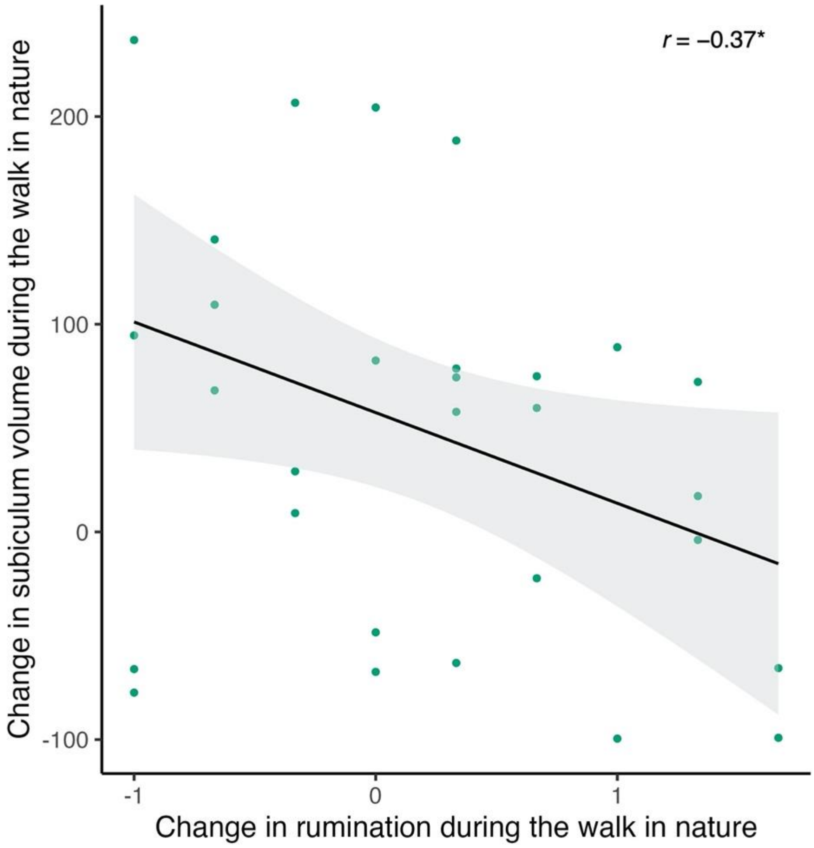


Figure 4. Negative correlation between the change in bilateral subiculum volume and the change in rumination during the walk in nature. During the walk in nature the increase in bilateral subiculum volume is associated with decreased rumination. *Note:* Significant differences are indicated with asterisk (*$p < 0.05$).

3. Discussion

The fact that we observe these short-term changes in brain structure, namely in the subiculum volume, is at odds with the typical assumption that brain structure, measured by means of MRI, is a relatively stable trait characteristic of an individual. However, there is increasing evidence hinting at short-term alterations of brain structure within the range of hours or even minutes [15], [16], [20], [21], [22]. For example, in a recent study in which participants were viewing pictures while structural images were taken in MRI, structural enlargement was found in the visual cortex after less than 263 seconds [23].

As the hippocampal formation has been related to upbringing environment [14] and its structure is highly plastic [16], we examined structural changes in hippocampal subfields after a one-hour walk in natural vs. urban environment. The results show that the walk in a forest caused an increase of subiculum volume in the hippocampal formation, whereas it remained stable after a walk in an urban environment. It should be noted that the environment-by-time interaction did not survive conservative Bonferroni correction for multiple comparisons, warranting a careful interpretation of these results and underscores the need for further investigation.

The role of hippocampal subfield subiculum has not been extensively studied, and its exact function remains unclear [24]. Except for its role in memory and spatial orientation [24], [25], [26], the subiculum, more specifically, the ventral subiculum, plays a role in inhibition of the stress-associated hypothalamic–pituitary–adrenal (HPA) axis [26], [27], [28], [29]. Furthermore, it has been suggested that the subiculum is involved in anxiety control [30]. This suggests that exposure to nature had a beneficial effect on a brain region which is involved in inhibiting stress responses and controlling anxiety. This is consistent with previous results reported from the same study showing that the forest walk decreased stress-related amygdala activity [11]. Therefore, a walk in nature, associated with a reduction in stress-related neural activity, may have led to the increase in subiculum volume, which in turn may be related to enhanced inhibition of the HPA axis and inhibition of stress responses. Given the role of the subiculum in processing spatial orientation [25], [26], it is as well plausible to speculate that the observed increase in subiculum volume could be associated with the task of navigating through a novel environment, such as a tranquil forest path. However, these hypotheses warrant further investigation to confirm their validity. It is important to note that the MRI methodology employed in this study, while providing valuable structural data, cannot directly identify the underlying biological mechanisms driving the observed change in subiculum volume after the nature walk [31]. To gain a more comprehensive understanding of these structural changes within biological tissues, future research may benefit from incorporating quantitative MRI or non-invasive in vivo histology techniques, which can offer additional insights into the nuances of such alterations [32].

Additionally, the increase in bilateral subiculum volume after the walk in nature was associated with a decrease in self-reported rumination. Even though the study was conducted in healthy participants, not in a clinical population, the results may be seen in line with a previous study showing a reduction in subiculum volume in patients with major depressive disorder, characterized by chronic exposure to stress and rumination [19], [33]. Additionally, reduction in subiculum volume has been associated with childhood maltreatment and mood disorders [34].

To our knowledge, this is the first intervention study to show evidence of structural brain plasticity after a short-term exposure to nature. Even though environment-by-time interaction in the bilateral subiculum was not maintained following Bonferroni correction, these are seminal findings hinting at a causal relationship between exposure to nature and brain plasticity and therefore we hold them as valuable. Additionally, the results show an association between the increase in subiculum volume and a reduction in rumination. These findings extend results of previous studies showing that rumination decreases after a walk in nature [9], [10] and those demonstrating that depression is associated with subiculum volume reduction [19], [33]. Since both, subiculum volume reduction and increased rumination are characteristics of major depressive disorder [19], [33], the results of this study, together with previous findings showing that nature decreases rumination [9], [10], may hint at the importance of spending time in nature as a potential preventive measure against the development of depression symptoms.

Nevertheless, since our sample consisted of healthy participants, further investigation in clinical populations is required to examine salutogenic effects of nature (forest in this case) for patients with depression in order to implement exposure to nature to clinical practice, such as green prescription [35]. As this is a seminal study to demonstrate salutogenic effect of a short-term exposure to nature on brain structure, we encourage future studies to continue exploring structural plasticity in the hippocampal formation, as well as other brain structures, as a result of exposure to natural environments with the aim to create solid evidence for use in clinical practice (e.g., green prescription), as well as urban and landscape planning.

Our study has several limitations. Firstly, as already mentioned, environment-by-time interaction in the bilateral subiculum fails to withstand the Bonferroni correction. However, as these are pioneering findings suggesting a plausible causal link between exposure to forest and brain plasticity, we hold them as valuable contribution to the field. Importantly, we encourage future studies to examine effects of exposure to natural vs. urban environments on the subiculum volume in a larger sample. Secondly, the mechanisms underlying the subiculum volume increase after walking in a natural environment remain unclear, and may be potentially influenced by factors like increased oxygen intake in a natural versus urban environment. Additionally, possible segmentation biases should be also considered. Thirdly, it remains unclear what natural features (e.g. the colour green, odours, sounds etc.) are driving the effect of the subiculum volume increase after the walk in nature. Fourthly, our sample mostly consisted of participant who were born and raised in Germany. Therefore, future studies should try to identify concrete active ingredients driving the effect, as well as include participants from different geographical and cultural backgrounds to enhance the generalizability of the findings.

4. Methods

2.1 Subjects

A sample size estimation using G*Power resulted in need of 54 participants to enable a medium effect size for a two-way mixed ANOVA, with an alpha level of 0.05. We decided to acquire 9 more participants to make sure that potential exclusion of participant or missing data would not reduce the sample size below the number that we decided on. We recruited 63 participants, who were pseudo-randomly assigned either to a forest walk or a city walk, while controlling for equal distribution of men and women. Participants reported their sex and ethnicity on a demographic self-report. Two participants were excluded due to missing data after the walk and one participant was excluded due to an error in image processing, resulting in total of 60 participants (29 women, total mean age = 27.31 years, *SD* = 6.74, age-range = 18−47 years, 30 participants in the nature walk condition, 30 participants in the urban walk condition). Out of the 60 participants 51 were from Germany (85%), 3 participants were from Russia (5%), one participant was from Greece, one participant from France, one from Ukraine, one from Brasil, and one from South Korea.

Participants' age, occupation, education, income and percentage of participants brought up in a city did not significantly differ between the two groups. An overview over the control variables in the two conditions is shown in Supplementary Table S2. Participants were told that they would take part in an MRI study in which they would go for a walk, but were not informed about the research question of the study. All participants were fluent in German, right-handed, and were not diagnosed with any psychological or neurological disorder.

The study was approved by the Local Psychological Ethical Committee at the Center for Psychosocial Medicine at University Medical Center Hamburg-Eppendorf in Hamburg, Germany (LPEK-0054). We obtained written informed consent from all participants and they received monetary compensation.

2.2 Study procedure

The experiment was conducted in late summer/fall 2019 between 10:00 a.m. and 5:00 p.m. The flowchart of the study procedure is shown in Figure 1. Upon arrival, participants signed the informed consent, filled out the questionnaires and performed a working memory task. Subsequently, the participants underwent an fMRI scanning procedure that included a resting state sequence with questions on rumination [36], [37], [38], a high-resolution hippocampal imaging sequence, the Fearful Faces Task [39], and the Montreal Imaging Stress Task [40]. The results on the Fearful Faces Task and the Montreal Imaging Stress Task were previously reported [11], [41].

After the scanning session, participants were randomly assigned to a 60-minute walk in either a natural or urban environment (Figure 2). Even though the definition and also the dichotomy of "natural" and "urban" environment has been a subject of debate [42], the "natural environment" we refer to is an urban forest, the largest green area in the city of Berlin, whereas "urban environment" refers to a busy street in one of the city centers in Berlin with shopping malls.

The participants were shown the walk on a map (straight path) and subsequently they were picked up at the lab and brought by taxi to the starting point of the walk. Participants went on the walk alone and were instructed not to enter shops or use their mobile phones, to avoid potential distraction. They were given a bagged lunch that they could eat during the walk. Participants were given a mobile phone that logged their global positioning system (GPS) data during the walk, to ensure that they walked the intended route (Figure 2a). After 30 minutes, an alarm signal went off on the phone, and participants were instructed to turn around and continued the walk back to the starting point. Here they were picked up by a taxi and brought back to the lab.

At posttest the same fMRI scanning procedure was repeated, with one additional stress-inducing task, the Social-Evaluative Threat task [43], also meant to induce social stress and administered only after the walk at the end of the MRI session, since we reasoned the cover story would not have been credible twice. Finally, participants filled out the questionnaires and were debriefed and informed about the aim of the study. The results of the analysis of the behavioural data as well as of the physiological data (electrodermal activity and heart rate) were previously reported [11].

2.3 Location of the walks

As recommended in a recent review [4], we report the geographic location of the walks as well as the landscape features. The walk in nature took place in Grunewald forest in Berlin, Germany (Figure 2b), close to the MRI laboratory (6.7 km, reached within approximately 15 minutes by taxi). The participants walked along Teltower Weg, a path starting at a crossroads between Königsweg and Teltower Weg, spanning towards the north of Grunewald. At over 3000 hectares, Grunewald forest is the largest green area in the city of Berlin. The vegetation of the area is mainly composed of conifers and Betulaceae. Some areas of Grunewald forest are nature reserves and therefore forbidden to visit to protect local fauna, especially amphibians and birds.

Apart from the river Havel which forms small islands and a peninsula, Grunewald forest is rich in lakes and ponds, however, the walking route did not pass any water. There are no built structures nor was there any traffic noise during the walking route the participants undertook. Since Grunewald is a recreative forest, it has many paths that people mostly use for walking, jogging, or riding a bicycle.

The urban walk took place in Schloßstraße, a busy street in Berlin-Steglitz (Figure 2c), close to the MRI laboratory (2.1 km, reachable in approximately 10 minutes by taxi), which consists of two to four traffic lanes. Schloßstraße is one of Berlin's shopping areas, with three shopping malls and three subway stations. Participants were dropped off by the taxi at Schloßstraße 84 and walked northeast, towards Rheinstraße. The participants walked along the sidewalk and could see other people, traffic, buildings, shopping malls, and smaller shops. In Schloßstraße, however, as in most of Berlin's streets, there were also trees, mostly on the sidewalk and on the traffic dividers.

2.4 Magnetic Resonance Imaging

2.4.1 Data acquisition

The structural images were acquired on a Siemens Tim Trio 3T scanner (Erlangen, Germany) using a 32-channel head coil. The T1 images were obtained using a three-dimensional T1-weighted magnetization prepared gradient-echo sequence (MPRAGE) based on the ADNI protocol (www.adni-info.org) (repetition time (TR) = 2500 ms; echo time (TE) = 4.77 ms; TI = 1100 ms, acquisition matrix = 256 × 256 × 176, flip angle = 7˚; 1 x 1 x 1 mm^3 voxel size). For the measurement of hippocampal subfields, a high resolution T2 weighted fast spin echo sequence (TR = 8150, TI = 50 ms, 0.4 x 0.4 mm in plane resolution, 2 mm slice thickness, 31 slices covering the anterior three quarters and in some cases the whole hippocampus)[44].

2.4.2 Hippocampus subfield segmentation

To obtain volumes of the hippocampal subfields we used in the post-processing the automated segmentation of hippocampal subfield (ASHS) tool [45]. The algorithm provides estimates of the following regions based on the UPenn atlas: CA1-3, dentate gyrus, subiculum, entorhinal cortex and parahippocampal gyrus, BA 35, BA36 and sulcus by means of method multi-atlas segmentation, similarity-weighted voting, and a novel learning-based bias correction technique. The tool has been shown to achieve excellent agreement with manual segmentation and with intra-class correlations comparable to the overlap between human evaluators in manual segmentations. As a quality check the segmentations were visually controlled. Before examining environment by time interaction, the subfields volumes were corrected for intracranial volume via the following linear equation: $ROI_{adj} = ROI_{vol} - \beta\ (ICV - ICV_{mean})$, where ROI_{adj} is the adjusted regional volume, ROI_{vol} is the original volume, and β is the slope of the ROI volume regressed on ICV as assessed by means of FreeSurfer and provided by ASHS, and ICV_{mean} is the sample mean of ICV[46]. There were no significant differences in intracranial volume between pretest and posttest (ICC = 0.97, 95% CI [0.94, 0.98]). The volume of the hippocampus and amygdala was calculated with FreeSurfer using the aseg command [47]. Descriptive statistics of regions of interest before and after the walk by environment are shown in Supplementary Table S2.

2.5 Rumination assessment

Rumination was conceptualized as repeatedly occurring thoughts that are unwanted or negative. They were measured by means of three items that have been used previously[36], [37], [38], of which two were adapted from the Stress Coping Inventory[48]. Participants were asked to rate how much the statements *"During the past five minutes, I could not get certain thoughts out of my mind."* and *"During the past five minutes, I kept thinking about something over and over again."* matched their thoughts and feelings. A third item was developed to capture self-related unwanted thoughts, *"During the past five minutes, I had difficulties suppressing thoughts about myself."*. Due to the constraints of the scanner environment were only able to use a 4-point answering scale, ranging from 0 (does not apply at all) to 3 (does apply very well), previously these items were used with a an 8-point answering scale. The assessment took place before and after the walk and directly after a five-minute resting state MRI acquisition. The average score across all three items was used for analysis, indicating the presence of unwanted thoughts across the resting state measurement.

2.6 Data analysis

Using a two-way mixed ANOVA with factors environment (urban vs. nature) and time (pre vs. post) we computed environment-by-time interactions to detect potential differential changes over time in the subfields of interests defined a priori: entorhinal cortex, associated with complex representations of the external environment [49], parahippocampal gyrus, previously shown to have higher volumes in adolescents raised exclusively in rural environments [14], and subiculum, involved in inhibition of hypothalamic-pituitary-adrenal (HPA) axis and stress response [26], using a Bonferroni corrected p-value of $p < 0.017$. Since a walk in nature reduces rumination [9], [10] and rumination in turn has been associated with the hippocampus [17], [18], [50], [51], we correlated change in the hippocampal subfield in which a significant environment-by-time interaction was observed with change in self-reported rumination [36], [37], [38] within both environments.

Data availability

The data supporting the findings of this study are available on a public repository at https://osf.io/xt2wn/

Code availibility

The code associated with the data analysis within this study is available on a public repository at https://osf.io/xt2wn/

Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

Author contributions

SS designed and coordinated the study, collected the data, performed data analysis and wrote the paper. SK had the idea for the study, designed and coordinated the study, supervised data acquisition, performed data analysis and reviewed the manuscript.

Acknowledgements

We are grateful for the assistance of the MRI team at the Max Planck for Human Development in Berlin consisting of Sonali Beckmann, Nadine Taube, Thomas Feg, Sebastian Schröder, Nils Bodammer and Davide Santoro and to Maike Hille, Emil Stobbe, Izabela Maria Sztuka, Carlos Raul Cassanello, Mirjam Reidick and Jakob Firnrohr for their help in collecting the data as well as to Nour Tawil for her help in creating the figures. This work was conducted at the Max Planck Dahlem Campus of Cognition (MPDCC) of the Max Planck Institute for Human Development, Berlin, Germany. During the work on her dissertation, Sonja Sudimac was a pre-doctoral fellow of the International Max Planck Research School on the Life Course (LIFE, www.imprs-life.mpg.de; participating institutions: Max Planck Institute for Human Development, Freie Universität Berlin, Humboldt-Universität zu Berlin, University of Michigan, University of Virginia, University of Zurich).

Declaration of interests

The authors declare no competing interests.

References

[1] J. Peen, J. Dekker, R. A. Schoevers, M. T. Have, R. De Graaf, and A. T. Beekman, ‘Is the prevalence of psychiatric disorders associated with urbanization?’, *Soc. Psychiatry Psychiatr. Epidemiol.*, vol. 42, no. 12, pp. 984–989, Dec. 2007, doi: 10.1007/s00127-007-0256-2.

[2] A. Ventriglio, J. Torales, J. M. Castaldelli-Maia, D. De Berardis, and D. Bhugra, ‘Urbanization and emerging mental health issues’, *CNS Spectr.*, vol. 26, no. 1, pp. 43–50, Feb. 2021, doi: 10.1017/S1092852920001236.

[3] M. P. White *et al.*, ‘Spending at least 120 minutes a week in nature is associated with good health and wellbeing’, *Sci. Rep.*, vol. 9, no. 1, p. 7730, Dec. 2019, doi: 10.1038/s41598-019-44097-3.

[4] M. R. Barnes, M. L. Donahue, B. L. Keeler, C. M. Shorb, T. Z. Mohtadi, and L. J. Shelby, ‘Characterizing nature and participant experience in studies of nature exposure for positive mental health: An integrative review’, *Front. Psychol.*, vol. 9, pp. 1–8, 2019, doi: 10.3389/fpsyg.2018.02617.

[5] R. Berto, ‘The role of nature in coping with psycho-physiological stress: A literature review on restorativeness’, *Behav. Sci.*, vol. 4, no. 4, pp. 394–409, Oct. 2014, doi: 10.3390/bs4040394.

[6] E. A. McMahan and D. Estes, ‘The effect of contact with natural environments on positive and negative affect: A meta-analysis’, *J. Posit. Psychol.*, vol. 10, no. 6, pp. 507–519, 2015, doi: 10.1080/17439760.2014.994224.

[7] J. Spasojević and L. B. Alloy, ‘Rumination as a common mechanism relating depressive risk factors to depression.’, *Emotion*, vol. 1, no. 1, p. 25, 2001, doi: 10.1037/1528-3542.1.1.25.

[8] E. R. Watkins, ‘Constructive and unconstructive repetitive thought.’, *Psychol. Bull.*, vol. 134, no. 2, p. 163, 2008, doi: 10.1037/0033-2909.134.2.163.

[9] G. N. Bratman, J. P. Hamilton, K. S. Hahn, G. C. Daily, and J. J. Gross, ‘Nature experience reduces rumination and subgenual prefrontal cortex activation’, *Proc. Natl. Acad. Sci.*, vol. 112, no. 28, pp. 8567–8572, Jul. 2015, doi: 10.1073/pnas.1510459112.

[10] S. Lopes, M. Lima, and K. Silva, ‘Nature can get it out of your mind: The rumination reducing effects of contact with nature and the mediating role of awe and mood’, *J. Environ. Psychol.*, vol. 71, pp. 1–7, Oct. 2020, doi: 10.1016/j.jenvp.2020.101489.

[11] S. Sudimac, V. Sale, and S. Kühn, ‘How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature’, *Mol. Psychiatry*, vol. 27, no. 11, pp. 4446–4452, Sep. 2022, doi: 10.1038/s41380-022-01720-6.

[12] M. Crous-Bou *et al.*, ‘Impact of urban environmental exposures on cognitive performance and brain structure of healthy individuals at risk for Alzheimer’s dementia’, *Environ. Int.*, vol. 138, pp. 1–10, May 2020, doi: 10.1016/j.envint.2020.105546.

[13] S. Kühn *et al.*, ‘Urban green is more than the absence of city: Structural and functional neural basis of urbanicity and green space in the neighbourhood of older adults’, *Landsc. Urban Plan.*, vol. 214, pp. 1–8, Oct. 2021, doi: 10.1016/j.landurbplan.2021.104196.

[14] S. Kühn *et al.*, ‘Brain structure and habitat: Do the brains of our children tell us where they have been brought up?’, *NeuroImage*, vol. 222, pp. 1–7, Nov. 2020, doi: 10.1016/j.neuroimage.2020.117225.

[15] S. Kühn *et al.*, ‘Spend time outdoors for your brain–an in-depth longitudinal MRI study’, *World J. Biol. Psychiatry*, pp. 1–7, 2021.

[16] Y. Sagi, I. Tavor, S. Hofstetter, S. Tzur-Moryosef, T. Blumenfeld-Katzir, and Y. Assaf, ‘Learning in the fast lane: New insights into neuroplasticity’, *Neuron*, vol. 73, no. 6, pp. 1195–1203, Mar. 2012, doi: 10.1016/j.neuron.2012.01.025.

[17] D. Mandell, G. J. Siegle, L. Shutt, J. Feldmiller, and M. E. Thase, ‘Neural substrates of trait ruminations in depression.’, *J. Abnorm. Psychol.*, vol. 123, no. 1, pp. 35–48, Feb. 2014, doi: 10.1037/a0035834.
[18] C. A. Figueroa, R. J. Mocking, G. van Wingen, S. Martens, H. G. Ruhe, and A. H. Schene, ‘Aberrant default-mode network-hippocampus connectivity after sad memory-recall in remitted-depression’, *Soc. Cogn. Affect. Neurosci.*, vol. 12, no. 11, pp. 1803–1813, 2017.
[19] E. V. Harel, R. L. Tennyson, M. Fava, and M. Bar, ‘Linking major depression and the neural substrates of associative processing’, *Cogn. Affect. Behav. Neurosci.*, vol. 16, no. 6, pp. 1017–1026, Dec. 2016, doi: 10.3758/s13415-016-0449-9.
[20] J. D. Karch *et al.*, ‘Identifying predictors of within-person variance in MRI-based brain volume estimates’, *NeuroImage*, vol. 200, pp. 575–589, Oct. 2019, doi: 10.1016/j.neuroimage.2019.05.030.
[21] H. Tost *et al.*, ‘Acute D2 receptor blockade induces rapid, reversible remodeling in human cortical-striatal circuits’, *Nat. Neurosci.*, vol. 13, no. 8, pp. 920–922, Aug. 2010, doi: 10.1038/nn.2572.
[22] M. Taubert, J. Mehnert, B. Pleger, and A. Villringer, ‘Rapid and specific gray matter changes in M1 induced by balance training’, *NeuroImage*, vol. 133, pp. 399–407, Jun. 2016, doi: 10.1016/j.neuroimage.2016.03.017.
[23] K. N. Månsson, D. S. Cortes, A. Manzouri, T.-Q. Li, S. Hau, and H. Fischer, ‘Viewing pictures triggers rapid morphological enlargement in the human visual cortex’, *Cereb. Cortex*, vol. 30, no. 3, pp. 851–857, 2020, doi: 10.1093/cercor/bhz131.
[24] A. Keresztes, L. Raffington, A. R. Bender, K. Bögl, C. Heim, and Y. L. Shing, ‘Longitudinal developmental trajectories do not follow cross-sectional age associations in hippocampal subfield and memory development’, *Dev. Cogn. Neurosci.*, vol. 54, p. 101085, Apr. 2022, doi: 10.1016/j.dcn.2022.101085.
[25] S. M. O’Mara, S. Commins, M. Anderson, and J. Gigg, ‘The subiculum: a review of form, physiology and function’, *Prog. Neurobiol.*, vol. 64, no. 2, pp. 129–155, Jun. 2001, doi: 10.1016/S0301-0082(00)00054-X.
[26] S. O’Mara, ‘The subiculum: what it does, what it might do, and what neuroanatomy has yet to tell us’, *J. Anat.*, vol. 207, no. 3, pp. 271–282, Sep. 2005, doi: 10.1111/j.1469-7580.2005.00446.x.
[27] J. Herman and N. Mueller, ‘Role of the ventral subiculum in stress integration’, *Behav. Brain Res.*, vol. 174, no. 2, pp. 215–224, Nov. 2006, doi: 10.1016/j.bbr.2006.05.035.
[28] C. A. Lowry, ‘Functional subsets of serotonergic neurones: Implications for control of the hypothalamic-pituitary-adrenal axis: Serotonergic systems and the HPA axis’, *J. Neuroendocrinol.*, vol. 14, no. 11, pp. 911–923, Nov. 2002, doi: 10.1046/j.1365-2826.2002.00861.x.
[29] N. K. Mueller, C. M. Dolgas, and J. P. Herman, ‘Stressor-selective role of the ventral subiculum in regulation of neuroendocrine stress responses’, *Endocrinology*, vol. 145, no. 8, pp. 3763–3768, Aug. 2004, doi: 10.1210/en.2004-0097.
[30] N. Mcnaughton, ‘The role of the subiculum within the behavioural inhibition system’, *Behav. Brain Res.*, vol. 174, no. 2, pp. 232–250, Nov. 2006, doi: 10.1016/j.bbr.2006.05.037.
[31] R. J. Zatorre, R. D. Fields, and H. Johansen-Berg, ‘Plasticity in gray and white: neuroimaging changes in brain structure during learning’, *Nat. Neurosci.*, vol. 15, no. 4, pp. 528–536, Apr. 2012, doi: 10.1038/nn.3045.
[32] N. Weiskopf, L. J. Edwards, G. Helms, S. Mohammadi, and E. Kirilina, ‘Quantitative magnetic resonance imaging of brain anatomy and in vivo histology’, *Nat. Rev. Phys.*, vol. 3, no. 8, pp. 570–588, Jun. 2021, doi: 10.1038/s42254-021-00326-1.

[33] K.-M. Han, E. Won, Y. Sim, and W.-S. Tae, ‘Hippocampal subfield analysis in medication-naïve female patients with major depressive disorder’, *J. Affect. Disord.*, vol. 194, pp. 21–29, Apr. 2016, doi: 10.1016/j.jad.2016.01.019.
[34] M. H. Teicher, C. M. Anderson, and A. Polcari, ‘Childhood maltreatment is associated with reduced volume in the hippocampal subfields CA3, dentate gyrus, and subiculum’, *Proc. Natl. Acad. Sci.*, vol. 109, no. 9, Feb. 2012, doi: 10.1073/pnas.1115396109.
[35] A. E. Van den Berg, ‘From green space to green prescriptions: Challenges and opportunities for research and practice’, *Front. Psychol.*, vol. 8, pp. 1–4, Feb. 2017, doi: 10.3389/fpsyg.2017.00268.
[36] A. Brose, F. Schmiedek, M. Lövdén, and U. Lindenberger, ‘Normal aging dampens the link between intrusive thoughts and negative affect in reaction to daily stressors.’, *Psychol. Aging*, vol. 26, no. 2, p. 488, 2011, doi: 10.1037/a0022287.
[37] S. Kühn, F. Schmiedek, A. Brose, B. H. Schott, U. Lindenberger, and M. Lövden, ‘The neural representation of intrusive thoughts’, *Soc. Cogn. Affect. Neurosci.*, vol. 8, no. 6, pp. 688–693, 2013, doi: 10.1093/scan/nss047.
[38] S. Kühn, M.-A. Vanderhasselt, R. De Raedt, and J. Gallinat, ‘The neural basis of unwanted thoughts during resting state’, *Soc. Cogn. Affect. Neurosci.*, vol. 9, no. 9, pp. 1320–1324, 2014, doi: 10.1093/scan/nst117.
[39] G. Mattavelli *et al.*, ‘Neural responses to facial expressions support the role of the amygdala in processing threat’, *Soc. Cogn. Affect. Neurosci.*, vol. 9, no. 11, pp. 1684–1689, 2014, doi: 10.1093/scan/nst162.
[40] K. Dedovic, R. Renwick, N. K. Mahani, V. Engert, S. J. Lupien, and J. C. Pruessner, ‘The Montreal Imaging Stress Task: using functional imaging to investigate the effects of perceiving and processing psychosocial stress in the human brain’, *J. Psychiatry Neurosci.*, vol. 30, no. 5, pp. 319–325, 2005.
[41] S. Sudimac and S. Kühn, ‘A one-hour walk in nature reduces amygdala activity in women, but not in men’, *Front. Psychol.*, vol. 13, pp. 1–13, Sep. 2022, doi: 10.3389/fpsyg.2022.931905.
[42] D. Karmanov and R. Hamel, ‘Assessing the restorative potential of contemporary urban environment (s): Beyond the nature versus urban dichotomy’, *Landsc. Urban Plan.*, vol. 86, no. 2, pp. 115–125, 2008, doi: 10.1016/j.landurbplan.2008.01.004.
[43] T. D. Wager, C. E. Waugh, M. Lindquist, D. C. Noll, B. L. Fredrickson, and S. F. Taylor, ‘Brain mediators of cardiovascular responses to social threat: part I: reciprocal dorsal and ventral sub-regions of the medial prefrontal cortex and heart-rate reactivity’, *Neuroimage*, vol. 47, no. 3, pp. 821–835, 2009, doi: 10.1016/j.neuroimage.2009.05.043.
[44] S. G. Mueller, L. L. Chao, B. Berman, and M. W. Weiner, ‘Evidence for functional specialization of hippocampal subfields detected by MR subfield volumetry on high resolution images at 4 T’, *Neuroimage*, vol. 56, no. 3, pp. 851–857, 2011, doi: 10.1016/j.neuroimage.2011.03.028.
[45] P. A. Yushkevich *et al.*, ‘Nearly automatic segmentation of hippocampal subfields in in vivo focal T2-weighted MRI’, *Neuroimage*, vol. 53, no. 4, pp. 1208–1224, 2010, doi: 10.1016/j.neuroimage.2010.06.040.
[46] N. Raz, A. M. Daugherty, A. R. Bender, C. L. Dahle, and S. Land, ‘Volume of the hippocampal subfields in healthy adults: differential associations with age and a pro-inflammatory genetic variant’, *Brain Struct. Funct.*, vol. 220, no. 5, pp. 2663–2674, 2015.
[47] B. Fischl *et al.*, ‘Whole Brain Segmentation’, *Neuron*, vol. 33, no. 3, pp. 341–355, Jan. 2002, doi: 10.1016/S0896-6273(02)00569-X.
[48] W. Janke and G. Erdmann, *SVF 78: eine Kurzform des Stressverarbeitungsfragebogens SVF 120; Kurzbeschreibung und grundlegende Kennwerte; Manual*. Hogrefe, Verlag für Psychologie, 2002.

[49] E. S. Nilssen, T. P. Doan, M. J. Nigro, S. Ohara, and M. P. Witter, ‘Neurons and networks in the entorhinal cortex: A reappraisal of the lateral and medial entorhinal subdivisions mediating parallel cortical pathways’, *Hippocampus*, vol. 29, no. 12, pp. 1238–1254, 2019, doi: 10.1002/hipo.23145.
[50] T. F. Denson, W. C. Pedersen, J. Ronquillo, and A. S. Nandy, ‘The angry brain: Neural correlates of anger, angry rumination, and aggressive personality’, *J. Cogn. Neurosci.*, vol. 21, no. 4, pp. 734–744, 2009, doi: 10.1162/jocn.2009.21051.
[51] A. S. Heller and R. C. Bagot, ‘Is hippocampal replay a mechanism for anxiety and depression?’, *JAMA Psychiatry*, vol. 77, no. 4, pp. 431–432, 2020, doi: 10.1001/jamapsychiatry.2019.4788.

Supplementary Information

Supplementary Table S1: Descriptive statistics for hippocampal subfields volume before and after the walk in the urban and in the natural environment

ROI	**Mean ± *SD***			
	Urban (*n* = 30)		**Nature (*n* = 30)**	
	pretest	**posttest**	**pretest**	**posttest**
Enthorinal cortex	471.95 ± 79.97	471.48 ± 74.07	462.87 ± 78.57	475.92 ± 59.46
Parahippocampal gyrus	996.67 ± 125.55	1002.40 ± 126.32	1029.42 ± 143.02	1028.61 ± 134.11
Subiculum	774.40 ± 119.65	776.10 ± 101.36	766.42 ± 126.61	816.10 ± 133.00

Note: ROI = region of interest; *SD* = standard deviation

Supplementary Table S2: Control variables values in the urban and in the natural environment

Variable	Urban (n = 30; 14 women)	Nature (n = 30; 15 women)	$\chi2/t$	*df*	*P*
Age (mean ± *SD*)	28.73 ± 7.49	25.90 ± 5.67	1.65	54.01	0.104
Upbringing: grew up in a city (%)	57	67	0.63	1	0.426
Income: under 1250 euros (%)	70	87	2.45	1	0.117
Occupation: students (%)	63	73	0.69	1	0.405
Education: high school diploma (%)	90	90	0	1	1
Day time: afternoon sessions (%)	43	47	0.07	1	0.795
Temperature[a] (mean ± *SD*)	16.11 ± 5.19	14.76 ± 5.55	0.97	57.75	0.334
Humidity (%)	67.83 ± 17.97	70.93 ± 18.46	−0.66	57.96	0.512
Cloudiness[b] (mean ± *SD*)	5.70 ± 2.02	6.23 ± 1.87	−1.06	57.66	0.293
Sunny: minutes during 60-minute walk (mean ± *SD*)	31.17 ± 22.82	21.30 ± 22.48	1.69	57.99	0.097
Rainy: walks in the rain (%)	37	33	0.66	1	0.417

Note: Weather values refer to 60 minutes of the walking time; weather data were obtained from the German Meteorological Service (https://www.dwd.de/); *df* = degrees of freedom; *SD* = standard deviation

[a] Degrees Celsius (°C)

[b]Amount of cloudiness on an 8-point scale

D: Paper IV

Sudimac, S., Drewelies, J., De Weerth C.* & Kühn, S.* (2024). *Effects of a walk in a residential natural vs. urban environment on objective and subjective stress indicators in mothers and their infants.* PsyArXiv. https://doi.org/10.31234/osf.io/pz83m
[Manuscript under revision]

Effects of a walk in a residential natural vs. urban environment on objective and subjective stress indicators in mothers and their infants

Sonja Sudimac[1], Johanna Drewelies[1], Carolina de Weerth[2]* & Simone Kühn[1,3,4]*

*These authors share the last authorship.

Affiliations:

[1] Max Planck Institute for Human Development,
Lise Meitner Group for Environmental Neuroscience,
Lentzeallee 94, 14195 Berlin, Germany

[2] Radboud University Medical Center,
Donders Institute for Brain, Cognition and Behaviour,
Kapittelweg 29, 6525 GD Nijmegen, The Netherlands

[3] University Medical Center Hamburg-Eppendorf,
Department of Psychiatry and Psychotherapy,
Martinistr. 52, 20251 Hamburg, Germany

[4] Max Planck UCL Centre for Computational Psychiatry
and Ageing Research Berlin, Germany and London, UK,
Lentzeallee 94, 14195 Berlin, Germany

Corresponding author: Sonja Sudimac
e-mail: sudimac@mpib-berlin.mpg.de

Abstract

Despite growing evidence that nature positively influences mood and stress, its effects on young children, especially infants, are not well-understood. To explore this, we conducted an intervention study with 72 mother-infant dyads. Mothers and their infants went on two walks, one in a natural and the other in an urban residential environment. We assessed effects of the walks on both subjective and physiological stress indicators, including maternal self-reported stress levels, salivary cortisol in mothers and infants, and cortisol levels in mothers' breast milk.

No significant interaction was found between time and environment on objective and subjective stress indicators. However, a decrease in cortisol concentrations in mothers and infants during walks in both environments was observed, suggesting that the walking itself may have decreased cortisol. Exploratory results showed that maternal salivary cortisol levels continued to decrease up to one hour following a walk in a natural environment, but not after urban walks, hinting at beneficial stress-relieving effects of natural compared to urban environments at a later timepoint. Self-reported assessments also revealed a reduction in maternal stress levels in both environments, accompanied by heightened feelings of pleasantness and calmness. Moreover, during the walk in nature, mothers experienced an increase in mood valence and wakefulness, while mood arousal decreased (though no significant interactions were found).

These present findings indicate that walks in residential natural versus urban environments do not differ in how they affect objective and subjective indicators of stress in mothers and their infants. Additional exploratory analyses suggest that for mothers walking in nature may result in stress-relief, with these effects potentially manifesting after a delay. This study advances our knowledge of how environmental factors influence stress, which can guide urban design policies aimed at enhancing mental health for specific populations and age groups.

Keywords: stress, cortisol, natural environment, urban environment, mother-infant dyad

1. Introduction:

Numerous studies have consistently demonstrated the positive effects of nature on mental health in adults (Kondo et al., 2018; Kotera et al., 2022; Oh et al., 2017). Thus, more green areas in a neighborhood were associated with decreased symptoms of depression, anxiety, and stress (Beyer et al., 2014; Cox et al., 2017), while the frequency of nature visits was negatively associated with mental distress (White et al., 2021). Furthermore, various nature-based interventions have been shown to reduce stress in both healthy and clinical populations (Corazon et al., 2019; Vujcic et al., 2017).

The benefits of nature for stress reduction have been evidenced not only through self-report stress assessments but also using objective, physiological stress markers, such as the stress hormone cortisol. Cortisol is the primary glucocorticoid hormone produced by the hypothalamic-pituitary-adrenal (HPA) axis in stressful situations. Persistent high levels of cortisol can be disadvantageous for mental health (Radley et al., 2015). And indeed, previous research has demonstrated that living close to green spaces is associated with lower cortisol levels (Gidlow, Randall, et al., 2016; Roe et al., 2013; Ward Thompson et al., 2012), underscoring the potential mental health benefits of natural environments. Additionally, experimental studies investigating the causal relationship between exposure to nature and physiological indicators of stress demonstrated that nature exposure can reduce cortisol. A meta-analysis of studies investigating the effects of "forest bathing", immersing oneself in a forest, demonstrated that being in a forest lowered cortisol concentrations compared to pre-intervention levels and control groups (Antonelli et al., 2019). Furthermore, it has been shown that cortisol levels decreased in coronary artery disease patients after a walk in an urban park compared to a walk in an urban environment (Grazuleviciene et al., 2016). In order to examine effects of regular exposure to nature, Hunter and colleagues (2019) examined changes in cortisol concentrations in healthy participants after two months of going to nature at least 3 times a week, and found that salivary cortisol decreased more than 20% per hour of visiting a natural environment.

Cognitively, nature exposure has been demonstrated to improve working memory capacity (Berman et al., 2008) and reduce rumination (Bratman et al., 2015). Likewise, benefits in nature have been as well demonstrated in brain activity, namely as a reduction of rumination-related activity in the subgenual prefrontal cortex (Bratman et al., 2015) and stress-related amygdala activity after walking in a natural compared to an urban environment (Sudimac et al., 2022).

Even though numerous studies have shown that visiting nature is beneficial for mental health (Barnes et al., 2019; Corazon et al., 2019; Kondo et al., 2018; Kotera et al., 2022; McMahan & Estes, 2015; Oh et al., 2017), the evidence is more scarce in children. A recent review showed that greater exposure to nature in childhood was associated with increased physical activity and lower obesity risk as well as with lower risk of neurodevelopmental problems, such as inattentiveness (Islam et al., 2020). Moreover, more residential green space in childhood was linked to lower risk of mental disorders (Engemann et al., 2019). A study focusing on children aged 4 to 6 years revealed that living near urban parks was associated with fewer mental health problems in families where mothers had lower educational levels, whereas children of highly educated mothers showed an opposite pattern (Balseviciene et al., 2014). Similarly, a study examining the potential relationship between exposure to nature and brain structure in children showed that lifelong exposure to green space in 7-to-10-year-old children may be associated with larger brain volume in regions linked to working memory processing (Dadvand et al., 2018). Furthermore, lifelong exposure to green environment was related with better working memory, as well as with a reduction in inattentiveness.

A relationship between proximity to green spaces and beneficial health outcomes has been observed not only in childhood, but during intrauterine development as well. Indeed, a mother's exposure to nature during pregnancy has been found to be associated with increased infant birth weight and reduced risk of preterm birth, especially in families with lower socio-economic status (Islam et al., 2020). Furthermore, it has been observed that pregnant women with low cortisol concentrations in the umbilical cord, relative to those with high cortisol, resided in a neighbourhood with higher residential green space, spent more time in the natural environment, had window views in their homes covered mostly with green space and more frequently looked at the green space through the window (Boll et al., 2020). Since high cortisol concentrations during pregnancy are associated with unfavorable pregnancy outcomes (Caparros-Gonzalez et al., 2022), these findings imply that pregnant women's exposure to green spaces may contribute to favorable pregnancy outcomes and benefit child health, particularly in urban settings.

Even though most of the literature indicates a generally positive relationship between the exposure to green spaces and child developmental outcomes, our understanding of how natural and urban environments affect infants remains limited. A study involving over 1300 mother-child dyads found that children age 0-to-2 years living in areas with a higher degree of residential green space, exhibited better early childhood neurodevelopment (Liao et al., 2019).

This association was partially explained by reduced air pollution related to traffic, as indicated by mediation analysis. In a similar vein, in 12-month-olds, the housing density of urban environments was associated with increased physiological stress (decreased parasympathetic activity) at home (Wass et al., 2021). Furthermore, in a laboratory setting, the housing density of the infants' home postcodes was associated with their increased behavioural and physiological reactivity to an emotion elicitation task. This relationship was independent from socio-economic status and lifelong stressors, suggesting that dense urban environments may be detrimental not only for adults, but also for infants. Nevertheless, it should be pointed out that these studies are cross-sectional, and therefore a causal relationship between urban density and developmental outcomes cannot be inferred.

Infants may be influenced directly by the environment in which they spend time or live, but also indirectly through the influence of their primary caregiver. Mothers that are more stressed show higher concentrations of the hormone cortisol in their breast milk (Tekgündüz et al., 2023). Hence, if a mother is more stressed because of the environment she lives in, she may affect the infant through her breast milk cortisol. And indeed, mothers' breast milk cortisol has been associated with infant temperament, particularly with fear and negative affect in female infants (Glynn et al., 2007; Grey et al., 2013; Nolvi et al., 2018). These results imply that information about the stressfulness of the environment may be transmitted via cortisol in breast milk, thus molding infants' emotional response accordingly (Nolvi et al., 2018).

Altogether, the existing literature suggests that exposure to natural environments can reduce experienced stress, as well as physiological indicators of stress, such as cortisol. Findings to date suggest that proximity to nature may be advantageous for children's development, while residing in densely populated urban areas could adversely affect their stress levels. However, literature on the potential positive effects of nature in infants is as yet scarce, and the underlying mechanisms are yet to be uncovered. In addition, because most studies on children are cross-sectional, the causal relationship between environmental factors and outcomes cannot be established. Finally, it is important to recognie that children, and infants in particular, are embedded into a close social context, and therefore predominantly influenced by their parents. This factor should also be considered examining the environmental effects on infants.

The current study was set up to address these gaps and limitations by using an intervention study design. Its goal was to investigate potential differential effects of a walk in a natural vs. an urban environment on stress levels and mood in mothers and their infants. To enhance the ecological validity of the study, we focused on examining effects of residential environments, that mothers habitually visit with their infant when going for a walk. Stress in mothers was measured with self-reports, as well as with cortisol levels, both from mothers' saliva and breast milk. Breast milk cortisol was included with the goal of uncovering a potential mechanism through which a mother's walking environment may indirectly affect the infant (i.e., maternal stress might be transmitted to the infant via breast milk cortisol). Stress in infants was measured based on mother's reports about the infant's behaviour, as well as with the infant's salivary cortisol concentrations. A secondary goal was to examine potential effects of a walk in a natural vs. an urban environment on maternal cognitive markers, namely working memory performance, rumination, and perceived attention restoration. This last outcome is based on the Attention Restoration Theory (ART) which proposes that natural environments have restorative effects on attention, by engaging it in an effortless way (Kaplan, 1995). Exploratorily, we sought to examine the relationship between potential changes in cortisol concentrations during walks in natural vs. an urban settings and mothers' connectedness to nature, as well as with their environment during upbringing. These findings can be found in the Supplementary Information.

Hypotheses, study design, the dependent variables and planned analyses were a-priori predefined and preregistered and are publicly available (https://aspredicted.org/6qx4m.pdf). As preregistered, we predicted that exposure to a natural relative to an urban environment would decrease stress levels and improve mood in mothers and their infants. Additionally, we expected that the exposure to nature relative to an urban environment would decrease maternal rumination, as well as increase perceived attention restoration and working memory capacity. To our knowledge, this is the first study to examine causal relations between walks in natural and urban environments and stress levels in mother-infant dyads.

2. Materials and Methods

2.1 Participants

Participants were recruited through flyers at public places in Berlin where mothers or families get together (parks, kindergartens, child-friendly restaurants) and through social media platforms (e.g., Instagram, Facebook, nebenan.de). The sample consisted of 73 mothers (mean age = 33.3 years, *SD* = 5.0 years, age range = 23–50 years) and their 73 infants (25 females and one participant with missing data about infant's sex, mean age = 7.5 months, *SD* = 3.4, age range = 1.8–15.1 months). We initially included infants up to 12 months of age and accepted 5 more mother-child dyads with infants older than 12 months since mothers confirmed that their infant usually stayed in a pram for walks of approximately one hour. A sample size estimation using G*Power resulted in the need of 80 participants to enable a medium effect size using between-subjects design. However, in the beginning of the data collection we decided for a within-subjects design instead, due to the large interindividual differences in cortisol levels (Smyth et al., 1997) and the varying degrees of participants' fear of COVID-19 infection. Therefore, we included all interested participants until the end of the planned recruitment period, namely one year. In order to enable a medium effect size (0.25), with a power of 0.95 and CI = 95% in a within-subjects design, 36 participants would have been needed. Since the final sample consisted of 73 participants, the post-hoc power is 0.99 for a medium effect size (0.25) and 0.49 for a small effect size (0.10). The study included only mothers residing in Berlin who were fluent in German, had not been diagnosed with a mental or neurodegenerative disorder, did not report cognitive impairments or drug addiction, typically took their infants out in a pram, and lived within 20 min walking distance from a natural and urban environment. Different ways of holding a baby (e.g., baby carriers, holding in the arms) can affect both mothers' and infants' stress responses (Ionio et al., 2021). Therefore, including only mothers who usually go for a walk with their infant in a pram made the sample more uniform and ensured that going for a walk in a pram was not a novel experience for the infants, thereby minimizing variability and reducing potential noise in the data.

The study was approved by the psychological ethics committee at the Center for Psychosocial Medicine at University Medical Center Hamburg-Eppendorf in Hamburg, Germany (LPEK-0187). Mothers signed the informed consent for their own and their infant's participation in the study. All participating mothers received a monetary compensation and a T-shirt with the study logo for their infant.

2.2 Study procedure

The data for the study were collected between May 2021 and April 2022. We used a pre-post-test design with an experimental intervention (walk in an urban or in a natural environment) to control for baseline mood and stress. The study procedure overview is shown in Figure 1. Using a within-subject design, each mother-infant dyad went on walks in both urban and natural environments, scheduled on two separate days. Mothers were not informed where the second walk would take place until they completed the first walk, in order to avoid participant bias. The order of the walks (natural or urban environment) was counterbalanced between the participants. To increase the ecological validity of the intervention, we asked participants to go for a walk in a residential urban and natural environment known to them. Thus, for the natural environment condition, mothers were instructed to take a walk in a nearby park that they typically visit with their infant. For the urban environment condition, they were asked to walk along a nearby busy street with traffic they typically use for grocery shopping or similar activities.

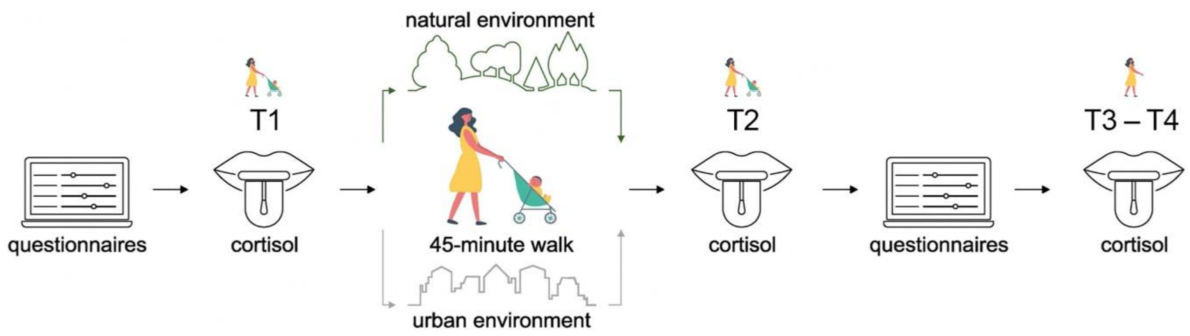


Figure 1. Study procedure overview. Before the walk mothers filled out questionnaires assessing their own and their infant's emotional states and collected saliva samples (T1). Afterwards, mothers went with the infant in a pram through urban and natural environments on different days, with the order of environments being randomised. Upon their return from the walk, mothers collected saliva samples again (T2), as well as a breast milk sample. Mothers then again filled out the same questionnaires, and collected additional saliva samples from themselves at intervals of 30 (T3) and 60 minutes (T4) after T2. The figure is adapted from "How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature" by Sudimac et al., 2022, *Molecular Psychiatry, 27*, p. 4448

Participants agreed with an experimenter on the exact route of the first walk, which was then provided to them as a digital map via e-mail. Before going on the walk participants were contacted by phone to ensure that they correctly understood the instructions, as well as how to collect and store the saliva and the milk sample. Participants received necessary materials as well as the instructions for collecting saliva and breast milk samples by post. Using these instructions, mothers collected their saliva and their infant's saliva themselves. Additionally, mothers who were breastfeeding (n = 55) collected a sample of breast milk. After the first walk, participants received the information about the second walk and a link for the online questionnaires for the second walk.

The entire study procedure was carried out by participants themselves, although they were given the option to contact the experimenters via e-mail or phone at any time. This approach was chosen mainly to enhance the ecological validity of the study, focusing on the effects of a walk in an everyday setting, but it was also affected by the limitations imposed by the COVID-19 pandemic. Mothers chose the day when they wanted to go for a walk and informed the experimenters. The median time interval between the two walks was 9.5 days (range: 1–109 days). They were instructed to go for a walk in the afternoon, between 13h and

17h, as cortisol levels are more stable in the afternoon than in the morning (Hansen et al., 2008). On the day of the experiment, before the walk, mothers filled out an online questionnaire about their mood, stress, rumination, and their infants' behaviour, and completed a working memory task. Subsequently, they collected their and their infant's saliva (timepoint T1), and, after placing their infant in a pram, proceeded to the prearranged route for a walk in an urban or in a natural environment. Participants received a GPS device by post that they took with them during the walk, to ensure that they walked the assigned route. Unfortunately, 40% of participants forgot to use the device during walks and therefore the GPS data could not be used in our analyses. The study walk was intended to last 45 minutes, with an additional 10–20 minutes to walk from the participants' home to the beginning of the route and back. Thus, mothers were instructed to set their mobile phone alarm to 22 minutes from the moment of starting their walk in the assigned environment, such as at the beginning of the park route for the natural environment and at the beginning of a street for an urban environment. Upon hearing the alarm, participants returned home using the same route, resulting in a total exposure time of 45 minutes to either an urban or natural environment. The average walk was 50 minutes long (mean = 50 minutes, SD = 12.5 minutes), and the duration of the walk did not significantly differ between the urban environment (mean duration = 50 minutes, *SD* = 8 minutes) and the natural environment (mean duration = 51 minutes, *SD* = 14 minutes; $t(87.28) = -0.68$; $p = 0.501$).

Upon their return from the walk, mothers again collected their own and their infants' saliva (timepoint T2), as well as their breast milk. Additionally, mothers collected their own saliva again 30 minutes (T3) and 60 minutes (T4) after timepoint T2. After collecting the first saliva sample after the walk (timepoint T2), mothers completed the same questionnaire used prior to the walk and again carried out the working memory task. Finally, they reported their perceived attention restoration after the walk, filled out a socio-demographic questionnaire, and answered questions about the walk. Mothers stored the saliva and breast milk samples in their freezers (-20°C) until experimenters collected the material and stored it in a freezer in the laboratory. Infants' saliva samples were centrifuged and together with maternal saliva and breast milk samples sent for further analysis. In the saliva samples we measured cortisol and in the breast milk samples cortisol and cortisone.

2.3 Measures

2.3.1 Behavioural measures

Maternal stress. Stress in mothers was assessed with the Negative Affect Schedule scale from the short version of the Positive and Negative Affect Schedule (PANAS) (Karim et al., 2011), consisting of 5 items, edited to include additional high-arousal items ('distressed' and 'irritable' instead of 'ashamed' and 'hostile'). The items in the scale are: upset, nervous, afraid, distressed, and irritable. The scale ranges from 1 to 5, with higher values indicating higher Maternal stress.

Maternal mood – Positive affect. Positive affect was measured using the Positive Affect Schedule scale in the short form of the PANAS (Karim et al., 2011). Positive Affect Schedule scale on PANAS consists of 5 items and values can range from 1 to 5. The items in the scale are: alert, inspired, determined, attentive, and active. Higher values indicate higher Positive affect.

Maternal mood – Valence and Arousal. Mood valence and arousal were assessed using a short version of Emotional Recall Task (ERT) (Li et al., 2020), in which participants were asked to write down 5 words to describe feelings they were experiencing at the moment and then to use the visual analog scale from 0 to 100 to indicate to what extent they were experiencing each of the stated feelings. Subsequently, participants evaluated each of the feelings on the Valence scale from 'unpleasant' to 'pleasant' and on the Arousal scale, from 'calm' to 'excited'. Valence and the Arousal scales can range from to –4 to +4. Negative values indicate negative valence and lower arousal, whereas positive values indicate positive valence and higher arousal.

Maternal mood – Pleasantness, Calmness and Wakefulness. Pleasantness, Calmness and Wakefulness were measured using a short version of the Multidimensional Mood Questionnaire (MMQ) (Hinz, 2012). The MMQ consists of 12 adjectives rated on a 6-point Likert scale (from 'definitely not' to 'extremely') that measure three dimensions: Pleasantness (pleasantness–unpleasantness), Calmness (calm–restless), and Wakefulness (awake–sleepy). All the scales can range from 1 to 5 with higher values indicating higher pleasantness, calmness and, wakefulness.

Rumination. Maternal trait rumination was assessed with the Rumination section of the Reflection Rumination Questionnaire (RRQ) (Elkhaouda, 2010). Participants answered how they have been feeling lately on the items such as "I always seem to be rehashing in my mind recent things I've said or done" on a scale from 1 to 5. The Rumination questionnaire consists of 12 items and the scale can range from 12 to 60 with higher values indicating higher trait rumination.

Working memory capacity. We used a visual version of the Digit Span Backwards task with performance-adapted adjustment (DSB) (Bowden et al., 2013) to assess mothers' working memory capacity. The score can range from 0 to 14, with higher score indicating better working memory capacity.

Perceived attention restoration. Perceived attention restoration was measured with Perceived Restorativeness Scale (PRS) (Schönbauer, 2013). The scale consists of 12 items and it can range from 1 to 11. Higher values on the scale indicate higher attention restoration.

Connectedness to nature. Connectednesss to nature was measured by means of the Connectedness with nature scale (Cervinka et al., 2009). It consists of 13 items and it can range from 13 to 65, with higher values indicating higher connectedness to nature.

Early-life urbanicity. Early-life urbanicity assesses urban upbringing, quantifying it as follows: number of years spent in a city (population over 100,000 inhabitants) before age 15, multiplied by 3, plus years spent in a town (population between 10,000 and 100,000 inhabitants) multiplied by 2, plus years spent in a rural environment (Lederbogen et al., 2011). This method aims to provide a weighted measure of early-life exposure to varying degrees of urban environments. It can range from 15 to 45 with higher values indicating higher early-life urbanicity.

Infant behaviour – Stress and Arousal. Infant behaviour was measured with Stress Arousal Checklist (SACL) (McCormick et al., 1985) in which mothers reported their infants' stress and arousal. The SACL consists of 30 adjectives describing emotions on a 4-point Likert scale, that are classified into two separate subscales: arousal (12 items) and stress (18 items). The scales can range from 1 to 4. Higher values on these subscales respectively indicates increased arousal and stress.

All behavioural measures, as well as the working memory task were completed before and after the walk, except for the Perceived Restorativeness Scale, Connectedness to nature, and Early-life urbanicity, assessed only after the walk.

2.3.2 Physiological measures

Stress levels were measured physiologically with glucocorticoid concentrations in mothers' and infants' saliva (i.e., cortisol), as well as in mothers' breast milk (i.e., cortisol and cortisone). Maternal saliva samples were collected through passive drooling using provided tubes and a short straw. Cortisol concentrations were determined using immunoassay (LabService, Dresden, Germany) and expressed in nanomoles per liter (nmol/L). Saliva samples were frozen and stored at –20 degrees Celsius until analysis. After thawing, samples were centrifuged at 3,000 rpm for 5 min, which resulted in a clear supernatant of low viscosity. Salivary concentrations were measured using commercially available chemiluminescence immunoassay with high sensitivity (Tecan – IBL International, Hamburg, Germany; catalogue number R62111). The intra-assay coefficient of variance was 2.1% and inter-assay coefficients of variance was 3.9%.

Mothers collected their own saliva samples at four time points: T1 – at pretest, and three times at posttest: T2 – directly after the walk, T3 – around 30 minutes after T2, T4 – around 60 minutes after T2. Mothers collected saliva samples from their babies using an eye sponge (De Weerth et al., 2007) placed in the baby's mouth before and after the walk (T1 and T2).

Milk cortisol determinations were carried out by analysing cortisol and cortisone in mothers' breast milk in the subsample of mothers who breastfed, with collections made only after the walk. Breast milk samples were processed and hormone levels of cortisol and cortisone were measured at the Endocrinology Laboratory of UMC Utrecht, Netherlands.

2.4 Data Analysis

2.4.1 Behavioural measures

Missing data. Data of two participants on behavioural measures were not recorded, whereas five participants were excluded from the analyses because they went for a walk to a route different than the one that was assigned to them. One participant was excluded from the behavioural data analysis because she only participated in the first walk. Data of four participants were excluded from the analysis in the working memory task (DSB) as they reported that they were distracted by their infant during the task. Thus, the final sample in the analysis of behavioural data consisted of 61 participants for the working memory task and 65 participants for all remaining tasks.

Outliers. As preregistered, the participants who scored 3 standard deviations (SD) below or above the mean were treated as outliers and were winsorised. In the MMQ three such outliers were identified and subsequently winsorised. One outlier was detected in the DSB task and winsorised.

Statistical analyses. Self-reports (PANAS, ERT, MMQ, RRQ, SACL) and the working memory task (DSB) that were administered before and after the walk were analysed with two-way repeated-measures ANOVA with within-subject factors time (pre vs. post) and environment (urban vs. nature). The dimension Wakefulness in the MMQ met the normality assumption and was analysed with ezANOVA from the package *ez* (Lawrence & Lawrence, 2016). Measures that were not normally distributed (PANAS, dimensions Pleasantness and Calmness in the MMQ, RRQ, DSB, and SACL) were analysed using non-parametric ANOVA from the R package *WRS2* (Mair & Wilcox, 2020). PRS, administered only after the walk, was analysed with the Wilcoxon test.

Additionally, sensitivity analyses were performed by repeating the analyses when excluding the participants who reported irregularities in the study protocol that might have impacted score on the questionnaires. These irregularities included: using mobile phone more than 10 minutes during the walk (4 participants), experiencing irregularities that could have affected stress levels during the walk (4 participants), walking on a weekend (1 participant), and going for a walk on the same route more than twice, potentially leading to increased familiarity with the study protocol (2 participants). Upon reanalysis excluding these participant groups, the outcomes remained consistent. Thus, for enhanced statistical power, the results presented include the entire sample.

In the analysis of covariance (ANCOVA), covariates were selected based on variables that showed significant differences between urban and natural environments. They included increased mothers' fear of COVID-19 infection after the urban walk ($t(83.85) = 2.91$; $p = 0.005$), as well as more sunlight ($t(125.48) = 2.75$; $p = 0.007$) during urban walks compared to those in natural settings. Despite integrating these factors — COVID-19 infection fear and sunlight —as covariates in the analysis, the outcomes remained consistent with those obtained without considering these covariates. Therefore, we present the results from the analysis without these covariates.

2.4.2 Physiological measures

Missing data. In the analysis of maternal salivary cortisol, five participants deviated from their assigned walk and these walks were excluded from further analysis of maternal salivary cortisol. Due to insufficient maternal saliva volumes, data were missing for 35 time points. Nevertheless, participants with incomplete data or those who only participated in the first walk were not excluded, as multilevel modeling is capable of handling missing data. In the analysis of maternal cortisol and cortisone concentrations from the breast milk and infants' cortisol concentrations, five participants were excluded: four for walking a different route than assigned and one who participated only in the first walk. The breast milk sample was missing in one of the walks for three participants, therefore, they were excluded from the further analysis. Ten mothers did not breastfeed, resulting in the sample of 55 participants in the analysis of cortisol in mothers' breast milk. In the analysis of infant salivary cortisol 13 samples did not contain enough saliva for the analysis, therefore, their data were excluded from further analysis, resulting in a final sample of 54 infants (19 female, mean age = 7.7 months, *SD* = 3.25).

Outliers. Salivary cortisol concentrations in mothers were measured at four different times: T1, T2, T3, T4, resulting in 8 data points per participant. We detected 8 data points with scores higher than 3 SD above the mean and winsorised them. In the analysis of cortisol and cortisone concentrations in mothers' breast milk, one outlier was identified in cortisone values, whereas two outliers were identified in cortisol values and were therefore winsorised. Since in the analysis of infant salivary cortisol, cortisol levels in three participants were higher than 3 SD above the mean, their data were winsorised.

Statistical analyses. To examine whether the walk in a natural or an urban environment affected salivary cortisol concentrations in mothers, as physiological indicators of their state stress, we performed multilevel growth curve modeling using *lme4* package (Bates et al., 2015). An additional model was considered in which we used an indicator coding to depict walks during which irregularities were reported that may have affected cortisol concentrations: using phone more than 10 minutes during the walk (4 walks), irregularities during the walk that could have affected stress levels (4 walks), going for a walk on a weekend (1 walk), going for a walk more than twice, which may have led to higher familiarity with the protocol (3 walks), as well as collecting saliva at T1 before 12h (2 walks), and after 17h (1 walk). After adding these dummy coded variables as covariates in the model, the results remained stable. Therefore, according to the principle of parsimony, we present the results without these covariates.

In the breast milk analysis for cortisol and cortisone concentrations, the cortisone distribution adhered to the assumption of normality and was analysed using a paired-samples t-test. However, cortisol distribution did not fulfill the normality criteria and was therefore examined using the Wilcoxon test. In the analysis of infant salivary cortisol, where the data were not normally distributed, they were analysed using non-parametric ANOVA from the R package *WRS2* (Mair & Wilcox, 2020).

3. Results

3.1 Behavioural measures

3.1.1 Preliminary analyses

Descriptive statistics for the behavioural variables are presented in Table 1.

Table 1: Descriptive statistics of behavioural variables.

	Mean ± *SD*			
	Urban		Nature	
Variable	**Pre-walk**	**Post-walk**	**Pre-walk**	**Post-walk**
Maternal stress[a]	1.80 ± 1.00	1.40 ± 0.40	1.60 ± 1.0	1.20 ± 0.60
Maternal mood – Positive affect[a]	3.43 ± 0.85	3.37 ± 0.73	3.39 ± 0.73	3.28 ± 0.80
Maternal mood – Valence	0.51 ± 1.36	0.85 ± 1.36	0.52 1.33	1.27 ± 1.48
Maternal mood – Arousal	– 0.25 ± 1.16	– 0.48 ± 1.05	– 0.29 ± 1.11	– 0.81± 1.11
Maternal mood – Pleasantness[a]	4.00 ± 1.25	4.25 ± 1.00	4.25 ± 1.25	4.50 ± 0.75
Maternal mood – Calmness[a]	3.50 ± 1.25	3.75 ± 1.50	3.50 ± 1.50	4.00 ± 1.00
Maternal mood – Wakefulness	2.92 ± 0.98	3.11 ± 0.86	2.94 ± 0.97	3.23 ± 0.89
Rumination[a]	41.00 ± 12.00	40.00 ± 13.00	42.00 ± 14.00	40.00 ± 14.00
Working memory capacity[a]	2.50 ± 5.00	3.00 ± 4.00	3.00 ± 5.00	3.00 ± 5.00
Perceived restored attention[a]	–	4.00 ± 3.00	–	8.00 ± 4.00
Infant behaviour – Stress[a]	2.94 ± 0.67	3.00 ± 0.44	2.83 ± 0.67	3.06 ± 0.39
Infant behaviour – Arousal[a]	3.00 ± 1.50	3.00 ± 1.00	3.00 ± 1.25	3.25 ± 1.00

Note: SD = standard deviation; *IQR* = interquartile range.

[a]For variables with non-normal distributions, medians and interquartile range (IQR) values are provided.

3.1.2 Main analyses

Self-report measures were analysed with two-way repeated-measures ANOVA with within-subject factors time (pre vs. post) and environment (urban vs. nature), focusing on environment-by-time interaction. Despite our expectations, there was no significant environment-by-time interaction in maternal self-reported Stress ($F(1,64) = 0.56$; $p = 0.458$), Positive affect ($F(1,64) = 0.22$; $p = 0.640$), mood – Valence ($F(1,64) = 2.45$; $p < 0.122$), mood – Arousal ($F(1,64) = 1.40$; $p < 0.241$), Pleasantness ($F(1,64) = 0.63$; $p = 0.626$), Calmness ($F(1,64) = 1.85$; $p = 0.177$), Wakefulness ($F(1,64) = 0.43$; $p = 0.516$), Rumination ($F(1,60) = 0.04$; $p = 0.849$), and Working memory capacity ($F(1,64) = 0.17$; $p = 0.679$). However, mothers reported that the natural environment walk was more restorative than the urban environment walk (Z = – 5.89; $p < 0.001$). They also enjoyed the walk in the natural environment more than in the urban environment (Z = – 6.76; $p < 0.001$). Contrary to our expectations, we found no significant environment-by-time interaction in infants Stress ($F(1,64) = 1.28$; $p = 0.260$) or Arousal ($F(1,64) = 0.65$; $p = 0.423$).

3.1.3 Secondary analyses

Since we did not observe the results that we initially hypothesised and preregistered, we performed exploratory analyses to further examine the effects of walking in a natural vs. an urban environment on the behavioural data. We conducted post hoc t-tests to separately analyse the effects of walking in an urban and in a natural environment on behaviour.

Wilcoxon t-test revealed that Maternal stress significantly decreased during both walks: urban ($Z = -2.99$; $p = 0.003$) and natural ($Z = -4.59$; $p < 0.001$; Figure 2). On the other hand, Wilcoxon tests showed that Positive affect did not change during the walk in the urban ($Z = -0.77$; $p = 0.438$) nor the natural environment ($Z = -0.88$; $p = 0.377$; Table 1).

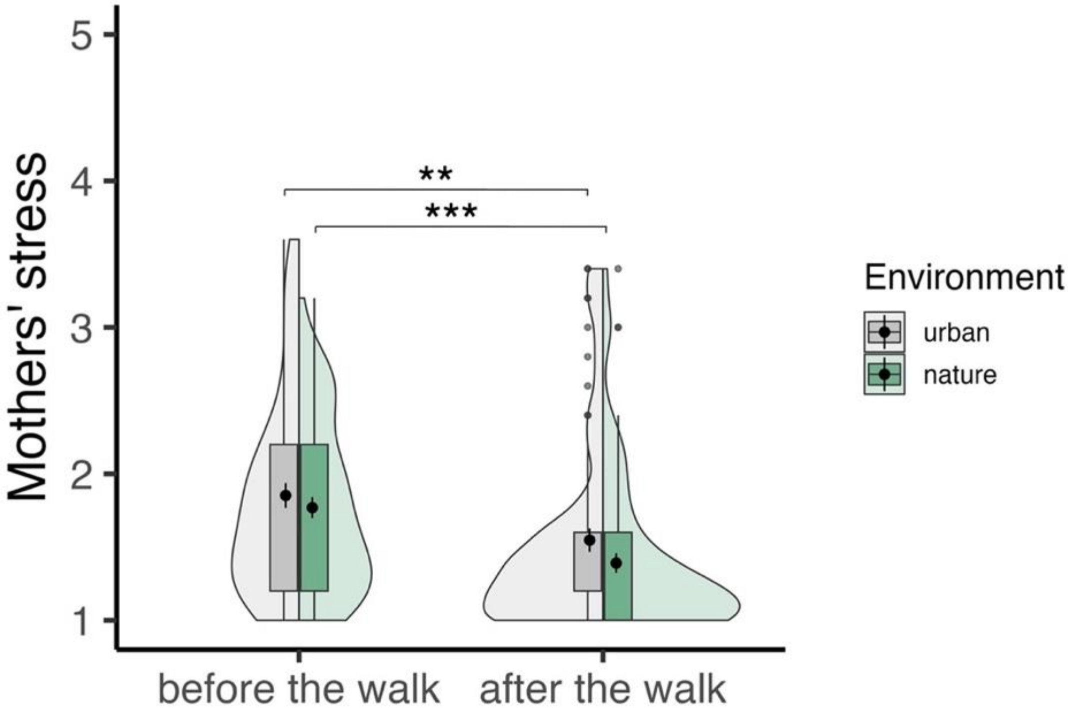


Figure 2. Maternal self-reported stress levels before and after a walk in an urban and in a natural environment. Maternal self-reported stress decreased during walks in both urban and natural environments.
Note: $^{**}p < 0.01$; $^{***}p < 0.001$

Post-hoc t-tests also revealed significantly increasing mood – Valence ($t(64) = -4.10$; $p < 0.001$; Figure 3a) and decreasing mood – Arousal ($t(64) = 2.98$; $p = 0.004$; Figure 3b) during the walk in the natural environment, whereas Valence ($t(64) = -1.52$; $p = 0.132$; Figure 3a) and Arousal ($t(64) = 1.65$; $p = 0.103$; Figure 3b) did not change during the urban walk.

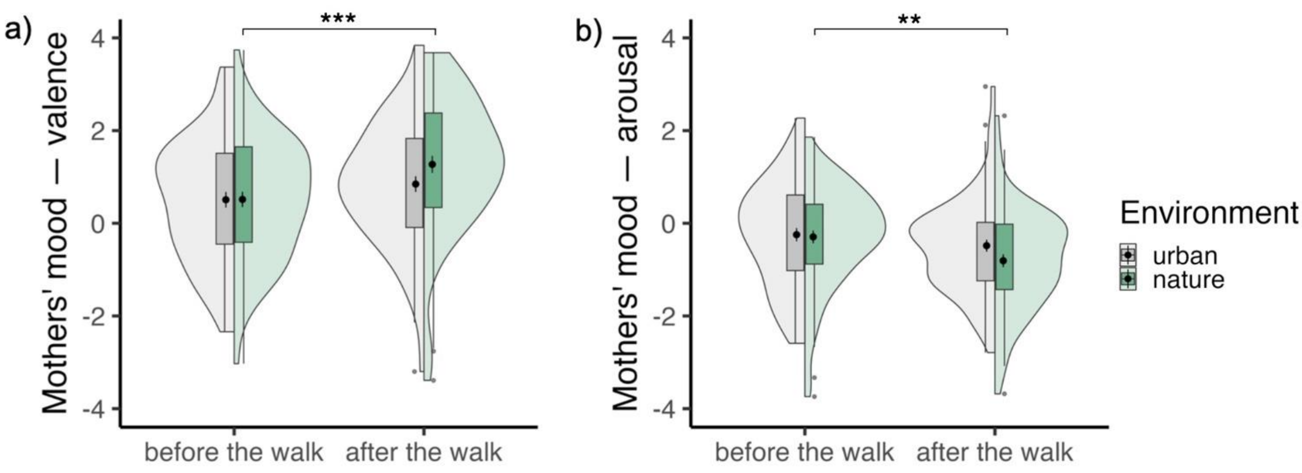


Figure 3. Maternal mood before and after a walk in an urban and in a natural environment. a) Maternal mood – Valence increased during a walk in nature, whereas it remained stable during an urban walk. b) Maternal mood – Arousal decreased during a walk in nature, whereas it remained stable during an urban walk.
Note: $^{**}p < 0.01$; $^{***}p < 0.001$

Additionally, post hoc t-test analyses revealed significant increases after both walks on Pleasantness: urban ($Z = -2.29$ $p < 0.022$) and natural ($Z = -3.48$; $p < 0.001$; Table 1), and in Calmness: urban ($Z = -3.02$; $p = 0.002$) and natural ($Z = -4.50$; $p < 0.001$; Table 1). However, significant increases in mothers' Wakefulness were found only after the natural walk ($t(64) = -2.47$; $p = 0.016$), and not the urban ($t(64) = -1.63$; $p = 0.108$; Table 1). Rumination significantly decreased in the urban environment ($Z = -2.12$ $p = 0.034$), but remained unchanged in the natural walk ($Z = -1.56$ $p = 0.118$; Table 1). Working memory did not change after both walks: urban ($Z = -0.19$; $p = 0.848$) and natural ($Z = -0.16$; $p = 0.869$; Table 1).

Post hoc t-test on infant behaviour revealed increases in Stress during the natural walk ($Z = -3.28$ $p = 0.001$), and no significant change in the urban walk ($Z = -1.44$ $p = 0.148$; Table 1), and no changes in Arousal after both walks: urban ($Z = -1.72$ $p = 0.086$) and natural ($Z = -0.65$ $p = 0.515$; Table 1).

In summary, the exploratory analyses showed that after both the walk in an urban and natural environment, mothers' Pleasantness and Calmness increased, whereas Maternal stress levels decreased. Furthermore, the findings indicated that walks in nature led to enhanced Maternal mood – Valence and Wakefulness, along with reduced Maternal mood – Arousal. Contrary to our expectations, mothers experienced a reduction in Rumination following the urban walk, while mothers reported higher infant Stress after the nature walk. Lastly, there were no observed changes in mothers' Positive affect or infant Arousal during either of the walks.

3.2 Physiological measures

3.2.1 Preliminary analyses

Within the preliminary analyses of maternal salivary cortisol, we first examined whether each timepoint differed between the natural and urban environments. Paired-samples t-tests revealed that cortisol concentrations did not significantly differ between the natural and urban environments at any time point (T1: ($t(62) = -1.47$; $p = 0.147$); T2: ($t(62) = -1.27$; $p = 0.209$); T3: ($t(60) = -1.60$; $p = 0.115$); T4: ($t(63) = 0.24$; $p = 0.813$). Descriptive statistics for maternal salivary cortisol at T1 to T4 are presented in Table 2, and the corresponding data are depicted in Figure 4. Further, we examined differences between time points within each environment. We performed paired-samples t-tests to examine whether there was potential change in cortisol concentrations after the walks (from point T1 to point T2). As presented on Figure 4, we observed a decrease in cortisol concentrations after the walk in both urban ($t(63) = 3.96$; $p < 0.001$) and natural environments ($t(61) = 4.34$; $p < 0.001$). It should be noted that salivary cortisol concentrations reflect cortisol from 20 to 30 minutes prior to the collection, indicating that a decrease in cortisol concentrations occurred towards the end of the walks. Further analysis showed that cortisol corrected for pre-walk levels (adjusted by subtracting cortisol levels at T1) between T2 and T4 decreased significantly only after the walk in nature ($t(64) = 3.08$; $p = 0.003$), but not after the walk in an urban environment ($t(66) = 0.60$; $p = 0.551$; Figure 4). Similarly, cortisol significantly dropped from T3 to T4, also only after the walk in nature ($t(63) = 2.23$; $p = 0.029$), whereas it remained unchanged after the urban walk($t(66) = 0.38$; $p = 0.704$; Figure 4). These findings suggest that the cortisol concentrations continued to decrease after the walk in nature, at least until one hour after the walk, while in the urban environment the cortisol only decreased from before to after the walk.

Table 2: Descriptive statistics of maternal salivary cortisol concentrations

	Urban				**Nature**			
Maternal salivary cortisol	**T1**	**T2**	**T3**	**T4**	**T1**	**T2**	**T3**	**T4**
Mean	3.18	2.51	2.33	2.24	3.65	2.85	2.64	2.22
SD	1.50	1.21	0.96	1.42	1.62	1.34	1.29	1.06

Note. SD = standard deviation.

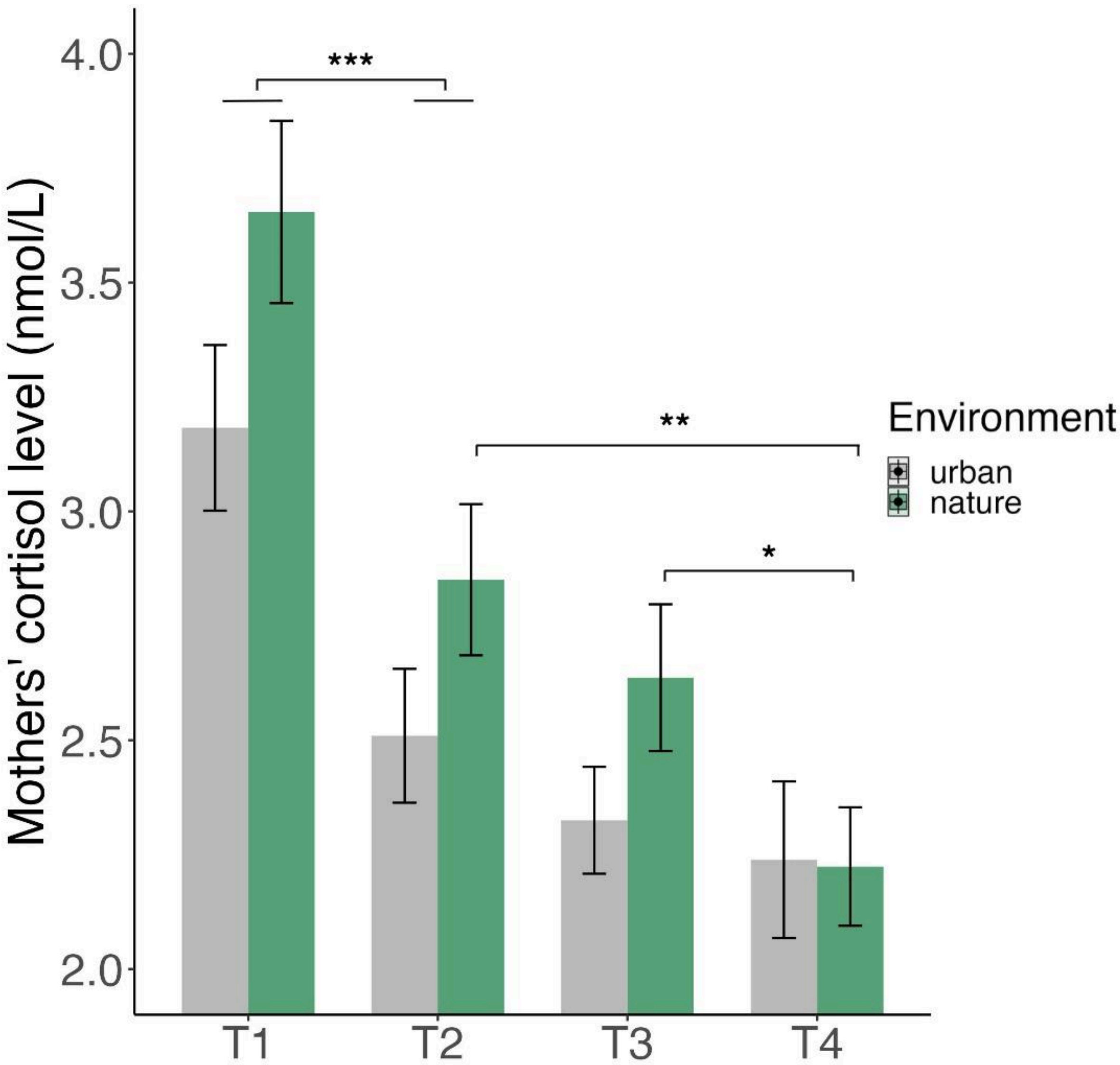


Figure 4. Mother salivary cortisol at time points T1–T4. Cortisol levels in mothers showed a significant decrease immediately after the walk (T2) compared to pre-walk levels (T1). After the walk in nature, cortisol levels significantly dropped from right after the walk (T2) and 30 minutes post-walk (T3) to 60 minutes post-walk (T4), whereas no change was observed following the walk in an urban environment after T2.
Note: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

3.2.2 Main analyses

Table 3 presents results from the multilevel model analyses on salivary cortisol concentrations in mothers. Firstly, in Model 1 we added linear time (time in minutes from collecting sample before the walk), quadratic time, the environment (urban and natural), and the interaction of the linear time and the environment. In Model 2, for reasons of parsimony, we incorporated only significant covariates, namely, variables that showed significant differences between the walk in an urban and in a natural environment. These included sunny weather, and fear of COVID-19 infection, as they may have influenced the changes in cortisol concentrations during the walks. Additionally, we controlled for self-reported Maternal stress before the walk, as a baseline of stress in mothers. The final model (Model 2) included 538 observations nested within 72 participants. Model 2 fit the data better (AIC: 1734.3, BIC: 1784.1) than Model 1 well (AIC: 1948.8, BIC: 1987.1).

Contrary to our initial hypothesis, the interaction between environment and time on maternal salivary cortisol concentrations did not reach significance in either Model 1 (p = 0.177) or Model 2 (p = 0.201). We observed a significant decrease in cortisol concentrations from T1 to T4 in both Model 1 (p = 0.003) and Model 2 (p = 0.007), meaning that the walk itself apparently had a cortisol-decreasing effect that was unrelated to where the walk took place (see Figure 4). Findings revealed that the covariate Sunny walk was negatively associated with cortisol concentrations, meaning that cortisol concentrations were lower when it was sunny weather. The covariate Fear of COVID-19 infection showed a negative correlation with cortisol concentrations, which might seem counterintuitive. However, this measure was not indicative of fear during the walk, but rather reflected participants' general concern about contracting COVID-19. It is possible that participants who had a greater fear of the virus might have found the walk more relaxing. It is important to acknowledge, though, that the number of COVID-19 cases varied during the data collection period, and for some participants, there was a gap of several weeks between the two walks. Therefore, their fear level might have been influenced by the prevailing case numbers at those specific times, which may have varied between the two walks.

Table 3: Multilevel growth curve model analyses of Maternal cortisol levels by Environment and Time (Model 1) and with covariates (Model 2)

	Model 1		Model 2	
	B **(SE)**	***t***	***B*** **(SE)**	***t***
Intercept	– 0.047 (0.157)	– 0.30	0.679 (0.308)	2.21*
Linear time	– 0.010 (0.004)	– 2.93**	– 0.009 (0.003)	– 2.70**
Quadratic time	0.000 (0.000)	1.58	– 0.000 (0.000)	1.15
Natural environment	0.023 (0.215)	0.11	0.129 (0.226)	0.58
Linear time × Natural environment	– 0.003 (0.002)	– 1.35	– 0.003 (0.002)	– 1.28
Maternal stress before the walk[a]	–	–	– 0.220 (0.133)	– 1.65
Sunny walk[b]	–	–	– 0.007 (0.002)	– 3.87***
Fear of COVID-19 infection[c]	–	–	– 0.009 (0.004)	– 2.16*

Note: B= prediction effect; *SE* = standard error
*$p < 0.05$
**$p < 0.01$
***$p < 0.001$

Table 4 presents the descriptive statistics for infant salivary cortisol, and the concentrations of cortisol and cortisone in mothers' breast milk.

Table 4: Descriptive statistics of infant salivary cortisol concentrations and cortisol and cortisone concentrations in mothers' breast milk.

	Mean ± *SD*			
	Urban		**Nature**	
Variable	**Pre-walk**	**Post-walk**	**Pre-walk**	**Post-walk**
Infant salivary cortisol[a]	2. 84 ± 2.47	1.69 ± 2.11	2.57 ± 2.23	1.89 ± 1.76
Breast milk cortisol[a]	–	2.30 ± 1.55	–	2.60 ± 2.30
Breast milk cortisone	–	13.76 ± 4.79	–	15.03 ± 5.39

Note. SD = standard deviation.

[a]For variables with non-normal distributions, median and interquartile range (IQR) values are provided.

Contrary to our hypothesis, the ANOVA revealed no environment-by-time interaction ($F(1,53) = 0.008$; $p = 0.930$) in infant salivary cortisol levels. Salivary cortisol in mothers and infants was positively associated before the walk ($r(126) = 0.18$, $p = 0.039$), but the association became marginally significant at T2, after the walk ($r(123) = 0.17$, $p = 0.065$).

The analysis of stress-related hormones in mothers' breast milk showed that there was likewise no difference after the walk from nature relative to the walk in an urban environment in mothers' breast milk cortisol ($Z = -1.72$, $p = 0.122$), or in cortisone concentrations ($t(54) = -1.56$, $p = 0.124$; Table 4). Cortisol in mothers' breast milk was positively associated with maternal salivary cortisol collected at the same time, after the walk ($r(106) = 0.49$, $p < 0.001$).

3.2.3 Secondary analyses

Since we did not observe the environment-by-time interaction in infant salivary cortisol levels, we performed post hoc t-tests to examine whether their cortisol levels changed after the walk in an urban and natural environment. The results revealed that infants' cortisol levels decreased after both the walk in nature ($Z = -2.19$, $p = 0.029$) as in the urban environment ($Z = -2.14$, $p = 0.033$; Figure 5).

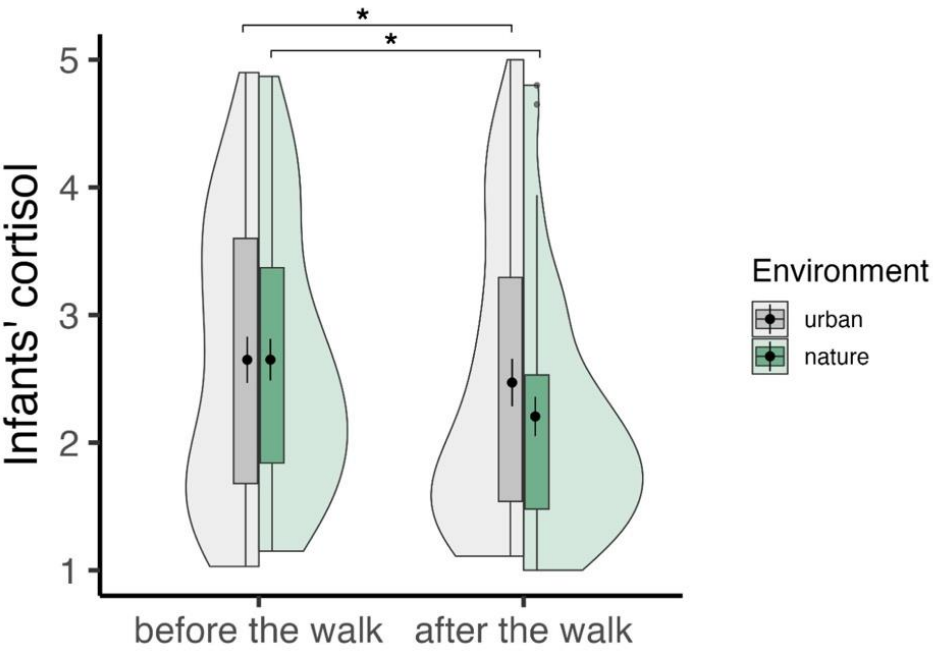


Figure 5. Infant salivary cortisol before and after a walk in an urban and in a natural environment. Infant salivary cortisol decreased during walks in both urban and natural environments.
Note: $^*p < 0.05$

4. Discussion

While numerous studies have demonstrated the mental health benefits of nature (Barnes et al., 2019; Corazon et al., 2019; Kondo et al., 2018; Kotera et al., 2022; McMahan & Estes, 2015; Oh et al., 2017) and its role in reducing cortisol levels (Antonelli et al., 2019; Chang et al., 2019), there has been a lack of research on the effects of exposure to residential natural and urban settings in children. To the best of our knowledge, this is the first study to investigate the causal link between a walk in residential natural vs. urban environments and both objective and subjective stress indicators in mothers and their infants.

Contrary to our preregistered hypotheses, we did not observe a significant interaction between environment and time in behavioural measures such as self-reported maternal stress, mood, working memory, and rumination, along with infants' stress and arousal. Similarly, no significant interaction was found in objective, physiological stress indicators, such as salivary cortisol concentrations in both mothers and infants, and cortisol and cortisone concentrations in maternal breastmilk. Nevertheless, mothers reported increased feelings of pleasantness and calmness after both walks, along with a decrease in stress. In line with this, the data did show a maternal and infant decrease in salivary cortisol concentrations from pre- to post-walk, but this was comparable in the natural and urban walks.

Several factors could account for the absence of the expected interaction between time and environment on both subjective and objective stress indicators. Regarding physiological indicators of stress, the results suggest that going on a walk, in general, reduced cortisol concentrations in mothers, implying that the walk itself, irrespective of the environment, may be beneficial for physiological indicators of stress. This aligns with previous studies (Gidlow, Jones, et al., 2016; Tyrväinen et al., 2014; Veitch et al., 2022), which also found no significant differences in cortisol levels when comparing walking in natural and urban environments, but observed cortisol decreases after walks in all environments. Furthermore, a systematic review shows that existing literature does not provide conclusive evidence that exposure to urban green spaces reduces physiological indicators of stress, including cortisol concentrations (Kondo et al., 2018). The key difference to previous studies showing larger cortisol decreases in natural vs. urban environments (Antonelli et al., 2019) is that they implemented a full day of forest immersions. This implies that longer immersion durations may be necessary to observe changes in cortisol levels. Moreover, in the previous studies reporting the effects of forest bathing on cortisol levels, the samples consisted of exclusively male participants (Kobayashi et al., 2012, 2019; B. J. Park et al., 2010; B.-J. Park et al., 2008, 2011; Tsunetsugu et al., 2010). Therefore, these findings might not be comparable to the results from the present study, consisting only of females. The analysis of cortisol in breast milk in a subsample of mothers who breastfed showed that breast milk cortisol concentrations also did not significantly differ between the urban and nature walk. However, due to challenges in collecting multiple breast milk samples in a short timeframe, we only obtained post-walk samples, preventing us from accounting for baseline breast milk cortisol levels. Importantly, cortisol concentrations in breast milk were associated with maternal salivary cortisol concentrations. Hence, the lack of significant differences between conditions in the breast milk cortisol and cortisone may be reflecting the lack of differences also found in maternal salivary cortisol.

Another potential reason for the lack of observed difference between walking in residential natural vs. urban environments on both physiological and subjective indicators of stress may be the location of the walks. Unlike prior studies focusing on stress reduction after a walk in natural vs. urban settings, where participants followed a predetermined path, our study sought ecological validity by assessing stress changes during walks along various routes in participants' residential environments. Thus, familiarity with these settings might have reduced the distinct impacts of natural and urban environments on stress. This leads to the question of whether more remote natural settings are required to fully experience the stress-reducing effects of nature, as suggested by forest bathing studies (Antonelli et al., 2019), as previous research on the effects of urban parks has not yet shown clear evidence of cortisol reduction (Kondo et al., 2018). Furthermore, going for a walk in wild nature has been found to decrease cortisol levels, compared to visiting an urban park or a built environment (Ewert & Chang, 2018). Thus, it seems that remote natural settings, abundant in natural elements like forests, might be essential to observe these stress-reducing effects on cortisol levels. Further studies are essential to determine whether visiting everyday urban green spaces may have beneficial effects on mental health as well. Additionally, high variability in environments along different paths, that were classified as "natural" or "urban" in our study, might have also played a role. Participants walked a range of different routes within both natural and urban environment, leading to a broader range of experiences compared to studies with a uniform path. Moreover, the residential environments in this study may be substantially different from environments in previous studies. For instance, urban settings in Berlin typically include streets with multiple car lanes and shops, but also a considerable number of trees, which might be different in other cities. This raises questions about the extent of natural features needed in an environment to yield stress-reduction benefits. An additional problem with the current experimental design may have been that many participants needed to go through urban areas to reach nearby parks, therefore their exposure to nature was interspersed with urban elements. The inevitable urban exposure in the nature walk condition might have impeded the potential stress-relieving impact of natural environments.

Another possible explanation for the absence of the interaction effect might be the current study's population of mothers and infants differed from that of previous studies. Furthermore, the presence of infants, who may have required care during the walks, might have influenced the mothers' stress levels, overshadowing environmental effects. The absence of observed effects on infants in our study could be attributed to the wide range of developmental stages in our sample (from 2 to 15 months) or to the possibility that the infants were too young to experience the positive impacts of nature. Therefore, future research should consider focusing on a more specific age range, include older children, or recruiting a large enough study population to study potential age effects.

A unique aspect of our study was that the mothers gathered data on their own, without the presence of an experimenter. While this approach was intended to better integrate the study into the participants' daily lives, thereby increasing ecological validity, navigating the study protocol alone may have caused stress for mothers, as also reported by some. This, in turn, could have interfered with the stress level outcomes resulting from the exposure to urban and natural environments. Yet, this factor was consistent across both natural and urban conditions, and since the order of walks was counterbalanced, any stress related to the study protocol should have been equally distributed between conditions.

Upon examining the differences in cortisol between each timepoint, our findings revealed a significant reduction in maternal cortisol concentrations from T2 to T4 (immediately after the walk to one hour post-walk) and from T3 to T4 (half an hour to one hour post-walk), but only following the walk in nature. No such change was observed after walking in an urban environment. Thus, cortisol concentrations seem to have continued to decrease at least until one hour after walking in nature, but not after urban walks. This may be interpreted as a hint that nature might have a larger stress-relieving effect compared to urban environments, but that this is only manifested later in time. However, further research is needed to replicate these findings and determine the duration of this effect.

Our exploratory analyses looking at self-reports separately for both walks, revealed that pleasantness and calmness in mothers increased after walks in both environments, whereas their stress levels decreased. This suggests that walking, regardless of the setting, had a positive effect on mothers' psychological wellbeing. This is in agreement with prior research, which demonstrated mood improvements and reduction of negative affect after walking in all three studied environments – natural settings, natural areas with water, and urban landscapes (Gidlow, Jones, et al., 2016; Tyrväinen et al., 2014).

Contrary to our expectation, positive affect in mothers did not change after either of the walks. However, in line with our hypothesis, mothers reported enhanced wakefulness and mood valence, along with reduced mood arousal after the walk in a natural, but not an urban environment. This discrepancy in self-reported outcomes, with no change in positive affect post-walk (as measured by PANAS), but an increase in mood valence and a decrease in arousal after the nature walk (as assessed by ERT), may stem from the differing ways of assessing mood in PANAS and ERT. In the ERT participants describe their affect themselves with adjectives that characterise how they feel at the very moment and then they rate these adjectives on valence and arousal. In contrast, PANAS focuses on a closed set of words (e.g. “inspired”, “determined”) where common emotions (e.g., “happy”) and items with low arousal are not present (Li et al., 2020). The PANAS may therefore be less suitable to assess mood changes after only one hour.

Opposite to what we anticipated, mothers experienced a reduction in rumination after the urban walk, whereas rumination did not change after the walk in nature. These findings contrast with prior research that reported a decrease in rumination after nature walks compared to urban walks (Bratman et al., 2015; Lopes et al., 2020). However, one of the differences between the previous studies and the present study is that mothers walked in familiar, residential environments, unlike predefined routes in the previous studies. Such familiarity might have provided more opportunities for social cues (e.g. seeing a neighbour) that may reduce feelings of isolation linked with rumination. Moreover, the diversity of stimuli in urban walks might have provided greater distraction from ruminative thoughts. Notably, in the present study, we measured rumination as a trait, inquiring how participants felt lately, rather than as a state rumination, which probes thoughts and feelings in the previous hour, as was done in previous studies (Bratman et al., 2015; Lopes et al., 2020). Capturing changes in trait rumination within a single day can be challenging, warranting cautious interpretation of the results. Additionally, the results revealed no change in mothers’ working memory capacity during the walks, consistent with several previous studies (De Brito et al., 2019; Koselka et al., 2019; Perkins et al., 2011), but differing from a study by Berman and colleagues (Berman et al., 2008). Our approaches differed in that we did not use a mental fatigue task prior to the walks and employed a visual, rather than verbal working memory task. This variation, along with our unique participant sample of mothers and infants walking in residential areas, and potential distractions by infants during the working memory task (despite excluding mothers who reported such distractions), may have influenced these results. Nevertheless, in alignment with our predictions and consistent with Attention Restoration Theory (Kaplan, 1995), mothers reported higher perceived attention restoration after walks in natural settings compared to urban ones. Consistent with this finding, they enjoyed the walk in nature more than the walk in an urban environment.

Contrary to our expectations, mothers observed no change in their infants’ arousal during the walk, but reported increased stress in infants after walks in nature. It may be that physical discomfort, such as uneven terrain, typical for urban parks may have led to discomfort for infants, perceived by mothers as higher stress. Nevertheless, it is important to note that infants’ arousal and stress were measured via mothers’ reports about infants’ behaviour and therefore may reflect their interpretation of the infants' emotional state. Further research in infants is necessary to examine whether, and in what way, their stress and mood change after exposure to natural and urban environments.

Exploratory analysis of infants' salivary cortisol revealed that cortisol levels in infants decreased during walks in both natural and urban settings. These results correspond with reduced salivary cortisol in mothers after both walks, and implies the walks' positive impact on infants' stress.

This study has several limitations. The distinct characteristics of natural and urban environments in Berlin raise questions about the comparability of routes across participants within each condition. Future studies using residential walking routes might benefit from examining specific environmental features, like tree coverage, as continuous variables, instead of broadly categorizing the settings of the walks as natural or urban. Additionally, most nature walks included exposure to urban areas, as participants navigated through them on the way to and from the natural settings. An additional limitation is the absence of objective data on the route and duration of the walks (GPS data), prohibiting us from linking objectively measured data, such as duration of the walk and environmental characteristics to the outcomes. A further potential constraint is the uneven sex distribution among infants, with only 25 of 73 being female. Future studies should aim for a more balanced distribution of males and females among infant participants to ensure broader applicability of the results and better understanding of sex-specific responses. Moreover, in our assessment of rumination during the walk, we used a survey designed to measure trait rumination, while measuring state rumination would have been more appropriate for this context. Therefore, we suggest that future studies focus on assessing how exposure to these environments impacts state rumination instead.

Further, even though the study protocol was designed for mothers to conduct independently in order to enhance ecological validity, future research might benefit from having an on-site experimenter to ensure study protocol uniformity and answer questions, potentially reducing additional stress elicited by the protocol. Collecting breast milk samples only after the walk did not enable us to account for baseline cortisol and cortisone. While it could be inconvenient for mothers to provide breast milk samples twice in such a short time span, future studies could include a subsample of participants willing to collect these samples both before and after the walk. Additionally, it remains uncertain whether lower cortisol concentrations in mothers and infants after walking in both natural and urban environments resulted from the walk itself or from daily cortisol fluctuations. Even though mothers went for a walk in the afternoon (from 13h to 17h), a period generally marked by more stable cortisol levels (Hansen et al., 2008), we cannot discard the possibility that the decrease in cortisol concentrations after the walk might be attributed to cortisol's diurnal rhythm, which typically diminishes throughout the day (Miller et al., 2016). Due to large differences in cortisol concentrations depending on the time of the day, future research should consider collecting an additional salivary cortisol sample before the walk, in order to establish a more stable cortisol baseline. Ideally, salivary cortisol samples within subsequent studies could be collected on several non-experimental days at various times, in order to examine whether the decrease in cortisol levels is impacted by the walk or present diurnal cortisol fluctuations. Finally, future studies should extend this field of investigation to father-infant dyads and other caregiver-child pairs.

5. Conclusions

In this study we investigated the causal effects of residential urban and natural environments on objective and subjective indicators of stress in mother-infant dyads during a one-hour walk. Our findings did not reveal any significant differences in physiological or self-reported stress levels between the urban and natural walks. We observed a decrease in cortisol concentrations after both walks in mothers and infants, suggesting that a walk in a residential environment had beneficial effects on objective indicators of stress, regardless of the type of the environment. Exploratory analysis of maternal self-reports revealed a decrease in stress levels in mothers after both walks, also suggesting that both walks had positive effects on stress reduction. These findings underscore the need for more research to understand how residential natural environments may benefit mother-infant dyads. The ultimate goal of this line of research is to inform urban design policies that can enhance mental health for diverse populations and age groups by contributing to the creation of optimal urban living spaces.

Data availability

The data supporting the findings of this study are publicly available at https://osf.io/ajqkc/

Code availability

The code associated with the data analysis within this study is publicly available at https://osf.io/ajqkc/

Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

Author contributions

S.S.: conceptualisation, study coordination, data collection, data curation, behavioural data analysis, physiological data analysis, visualization, interpretation; manuscript writing; J.D.: support for physiological data analysis; interpretation; manuscript review; C.W.: conceptualisation, supervision of data analysis, interpretation; manuscript review; S.K.: conceptualisation, supervision of data collection, supervision of data analysis, interpretation; manuscript review.

Acknowledgements

We are thankful to Elena Isenberg, Katharina Schmalen, Carmen Kaiser, Kağan Porsuk, Jordan Elias, Jona Carmon, Angela Fiedler, Kristin Witte, Lisa Berentelg, Laura Scherliess, and Elisa Stuewe for their help in collecting the data, as well to the participants in this study. We express our appreciation to Dr. Annette Brose for her insightful feedback at early stages of the project. We are also grateful to Hannah Kruft for her assistance in data preprocessing and to Nour Tawil for her contribution in creating the study logo, flyers and the figures. We thankfully acknowledge the use of an image sourced from iStock in the preparation of this publication. This work was conducted at the Max Planck Dahlem Campus of Cognition (MPDCC) of the Max Planck Institute for Human Development, Berlin, Germany. During the work on her dissertation, Sonja Sudimac was a pre-doctoral fellow of the International Max Planck Research School on the Life Course (LIFE, www.imprs-life.mpg.de; participating institutions: Max Planck Institute for Human Development, Freie Universität Berlin, Humboldt-Universität zu Berlin, University of Michigan, University of Virginia, University of Zurich).

Declaration of interests

The authors declare no competing interests.

References

Antonelli, M., Barbieri, G., & Donelli, D. (2019). Effects of forest bathing (shinrin-yoku) on levels of cortisol as a stress biomarker: A systematic review and meta-analysis. *International Journal of Biometeorology*, *63*(8), 1117–1134. https://doi.org/10.1007/s00484-019-01717-x

Balseviciene, B., Sinkariova, L., Grazuleviciene, R., Andrusaityte, S., Uzdanaviciute, I., Dedele, A., & Nieuwenhuijsen, M. (2014). Impact of residential greenness on preschool children's emotional and behavioral problems. *International Journal of Environmental Research and Public Health*, *11*(7), 6757–6770. https://doi.org/10.3390/ijerph110706757

Barnes, M. R., Donahue, M. L., Keeler, B. L., Shorb, C. M., Mohtadi, T. Z., & Shelby, L. J. (2019). Characterizing nature and participant experience in studies of nature exposure for positive mental health: An integrative review. *Frontiers in Psychology*, *9*, 1–8. https://doi.org/10.3389/fpsyg.2018.02617

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using **lme4**. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Berman, M. G., Jonides, J., & Kaplan, S. (2008). The cognitive benefits of interacting with nature. *Psychological Science*, *19*(12), 1207–1212. https://doi.org/10.1111/j.1467-9280.2008.02225.x

Beyer, K., Kaltenbach, A., Szabo, A., Bogar, S., Nieto, F., & Malecki, K. (2014). Exposure to neighborhood green space and mental health: Evidence from the survey of the health of Wisconsin. *International Journal of Environmental Research and Public Health*, *11*(3), 3453–3472. https://doi.org/10.3390/ijerph110303453

Boll, L. M., Khamirchi, R., Alonso, L., Llurba, E., Pozo, Ó. J., Miri, M., & Dadvand, P. (2020). Prenatal greenspace exposure and cord blood cortisol levels: A cross-sectional study in a middle-income country. *Environment International*, *144*, 1–11. https://doi.org/10.1016/j.envint.2020.106047

Bowden, S. C., Petrauskas, V. M., Bardenhagen, F. J., Meade, C. E., & Simpson, L. C. (2013). Exploring the dimensionality of digit span. *Assessment*, *20*(2), 188–198. https://doi.org/10.1177/1073191112457

Bratman, G. N., Hamilton, J. P., Hahn, K. S., Daily, G. C., & Gross, J. J. (2015). Nature experience reduces rumination and subgenual prefrontal cortex activation. *Proceedings of the National Academy of Sciences*, *112*(28), 8567–8572. https://doi.org/10.1073/pnas.1510459112

Caparros-Gonzalez, R. A., Lynn, F., Alderdice, F., & Peralta-Ramirez, M. I. (2022). Cortisol levels versus self-report stress measures during pregnancy as predictors of adverse infant outcomes: A systematic review. *Stress*, *25*(1), 189–212. https://doi.org/10.1080/10253890.2022.2059348

Cervinka, R., Zeidler, D., Karlegger, A., & Hefler, E. (2009). Connectedness with nature, well-being and time spent in nature. *Program and Abstract of 8th Biennial Conference, Environmental Psychology, September, 6th–9th (S. 130). Lengrich: Pabst Science Publishers*.

Chang, Y., Ewert, A., Kamendulis, L. M., & Hocevar, B. A. (2019). Measuring biophysical and psychological stress levels following visitation to three locations with differing levels of nature. *Journal of Visualized Experiments*, *148*, 1–9. https://doi.org/10.3791/59272

Corazon, S. S., Sidenius, U., Poulsen, D. V., Gramkow, M. C., & Stigsdotter, U. K. (2019). Psycho-physiological stress recovery in outdoor nature-based interventions: A systematic review of the past eight years of research. *International Journal of*

Environmental Research and Public Health, *16*(10), 1–21. https://doi.org/10.3390/ijerph16101711

Cox, D. T., Shanahan, D. F., Hudson, H. L., Plummer, K. E., Siriwardena, G. M., Fuller, R. A., Anderson, K., Hancock, S., & Gaston, K. J. (2017). Doses of neighborhood nature: The benefits for mental health of living with nature. *AIBS Bulletin*, *67*(2), 147–155.

Dadvand, P., Pujol, J., Macià, D., Martínez-Vilavella, G., Blanco-Hinojo, L., Mortamais, M., Alvarez-Pedrerol, M., Fenoll, R., Esnaola, M., Dalmau-Bueno, A., López-Vicente, M., Basagaña, X., Jerrett, M., Nieuwenhuijsen, M. J., & Sunyer, J. (2018). The association between lifelong greenspace exposure and 3-dimensional brain magnetic resonance imaging in Barcelona schoolchildren. *Environmental Health Perspectives*, *126*(2), 1–8. https://doi.org/10.1289/EHP1876

De Brito, J. N., Pope, Z. C., Mitchell, N. R., Schneider, I. E., Larson, J. M., Horton, T. H., & Pereira, M. A. (2019). Changes in psychological and cognitive outcomes after green versus suburban walking: A pilot crossover study. *International Journal of Environmental Research and Public Health*, *16*(16), 1–12. https://doi.org/10.3390/ijerph16162894

De Weerth, C., Jansen, J., Vos, M. H., Maitimu, I., & Lentjes, E. G. W. M. (2007). A new device for collecting saliva for cortisol determination. *Psychoneuroendocrinology*, *32*(8–10), 1144–1148. https://doi.org/10.1016/j.psyneuen.2007.07.005

Elkhaouda, S. (2010). *Geschlechtsspezifische Faktoren in der Vorhersage der Depressivität bei Jugendlichen* (R. de Jong-Meyer, Ed.; [Electronic ed.]). https://repositorium.uni-muenster.de/document/miami/c84b9ff7-650f-4e48-afa6-8f88d19fcdd8/diss_elkhaouda.pdf

Engemann, K., Pedersen, C. B., Arge, L., Tsirogiannis, C., Mortensen, P. B., & Svenning, J.-C. (2019). Residential green space in childhood is associated with lower risk of psychiatric disorders from adolescence into adulthood. *Proceedings of the National Academy of Sciences*, *116*(11), 5188–5193. https://doi.org/10.1073/pnas.1807504116

Ewert, A., & Chang, Y. (2018). Levels of nature and stress response. *Behavioral Sciences*, *8*(5), 1–13. https://doi.org/10.3390/bs8050049

Gidlow, C. J., Jones, M. V., Hurst, G., Masterson, D., Clark-Carter, D., Tarvainen, M. P., Smith, G., & Nieuwenhuijsen, M. (2016). Where to put your best foot forward: Psycho-physiological responses to walking in natural and urban environments. *Journal of Environmental Psychology*, *45*, 22–29. https://doi.org/10.1016/j.jenvp.2015.11.003

Gidlow, C. J., Randall, J., Gillman, J., Smith, G. R., & Jones, M. V. (2016). Natural environments and chronic stress measured by hair cortisol. *Landscape and Urban Planning*, *148*, 61–67. https://doi.org/10.1016/j.jenvp.2015.11.003

Glynn, L. M., Davis, E. P., Schetter, C. D., Chicz-DeMet, A., Hobel, C. J., & Sandman, C. A. (2007). Postnatal maternal cortisol levels predict temperament in healthy breastfed infants. *Early Human Development*, *83*(10), 675–681. https://doi.org/10.1016/j.earlhumdev.2007.01.003

Grazuleviciene, R., Vencloviene, J., Kubilius, R., Grizas, V., Danileviciute, A., Dedele, A., Andrusaityte, S., Vitkauskiene, A., Steponaviciute, R., & Nieuwenhuijsen, M. (2016). Tracking restoration of park and urban street settings in coronary artery disease patients. *International Journal of Environmental Research and Public Health*, *13*(6), 1–9. https://doi.org/10.3390/ijerph13060550

Grey, K. R., Davis, E. P., Sandman, C. A., & Glynn, L. M. (2013). Human milk cortisol is associated with infant temperament. *Psychoneuroendocrinology*, *38*(7), 1178–1185. https://doi.org/10.1016/j.psyneuen.2012.11.002

Hansen, Å. M., Garde, A. H., & Persson, R. (2008). Sources of biological and methodological variation in salivary cortisol and their impact on measurement among healthy adults:

A review. *Scandinavian Journal of Clinical and Laboratory Investigation*, *68*(6), 448–458. https://doi.org/10.1080/00365510701819127

Hinz, A. D., Isolde; Petrowski, Katja; Brähler, Elmar. (2012). Die Stimmung in der deutschen Bevölkerung: Referenzwerte für den Mehrdimensionalen Befindlichkeitsfragebogen MDBF. *PPmP - Psychotherapie · Psychosomatik · Medizinische Psychologie*, *62*(02), 52–57. https://doi.org/10.1055/s-0031-1297960

Hunter, M. R., Gillespie, B. W., & Chen, S. Y.-P. (2019). Urban nature experiences reduce stress in the context of daily life based on salivary biomarkers. *Frontiers in Psychology*, *10*, 1–16. https://doi.org/10.3389/fpsyg.2019.00722

Ionio, C., Ciuffo, G., & Landoni, M. (2021). Parent–infant skin-to-skin contact and stress regulation: A systematic review of the literature. *International Journal of Environmental Research and Public Health*, *18*(9), 1–14. https://doi.org/10.3390/ijerph18094695

Islam, M. Z., Johnston, J., & Sly, P. D. (2020). Green space and early childhood development: A systematic review. *Reviews on Environmental Health*, *35*(2), 189–200. https://doi.org/10.1515/reveh-2019-0046

Kaplan, S. (1995). The restorative benefits of nature: Toward an integrative framework. *Journal of Environmental Psychology*, *15*(3), 169–182. https://doi.org/10.1016/0272-4944(95)90001-2

Karim, J., Weisz, R., & Rehman, S. U. (2011). International positive and negative affect schedule short-form (I-PANAS-SF): Testing for factorial invariance across cultures. *Procedia - Social and Behavioral Sciences*, *15*, 2016–2022. https://doi.org/10.1016/j.sbspro.2011.04.046

Kobayashi, H., Park, B.-J., & Miyazaki, Y. (2012). Normative references of heart rate variability and salivary alpha-amylase in a healthy young male population. *Journal of Physiological Anthropology*, *31*(1), 1–8. https://doi.org/10.1186/1880-6805-31-9

Kobayashi, H., Song, C., Ikei, H., Park, B.-J., Kagawa, T., & Miyazaki, Y. (2019). Combined effect of walking and forest environment on salivary cortisol concentration. *Frontiers in Public Health*, *7*, 1–6. https://doi.org/10.3389/fpubh.2019.00376

Kondo, M., Fluehr, J., McKeon, T., & Branas, C. (2018). Urban green space and its impact on human health. *International Journal of Environmental Research and Public Health*, *15*(3), 1–28. https://doi.org/10.3390/ijerph15030445

Koselka, E. P. D., Weidner, L. C., Minasov, A., Berman, M. G., Leonard, W. R., Santoso, M. V., de Brito, J. N., Pope, Z. C., Pereira, M. A., & Horton, T. H. (2019). Walking Green: Developing an Evidence Base for Nature Prescriptions. *International Journal of Environmental Research and Public Health*, *16*(22), 4338. https://doi.org/10.3390/ijerph16224338

Kotera, Y., Richardson, M., & Sheffield, D. (2022). Effects of shinrin-yoku (forest bathing) and nature therapy on mental health: A systematic review and meta-analysis. *International Journal of Mental Health and Addiction*, *20*(1), 337–361. https://doi.org/10.1007/s11469-020-00363-4

Lawrence, M. A., & Lawrence, M. M. A. (2016). Package 'ez'. *R Package Version*, *4*(0).

Lederbogen, F., Kirsch, P., Haddad, L., Streit, F., Tost, H., Schuch, P., Wüst, S., Pruessner, J. C., Rietschel, M., Deuschle, M., & Meyer-Lindenberg, A. (2011). City living and urban upbringing affect neural social stress processing in humans. *Nature*, *474*(7352), 498–501. https://doi.org/10.1038/nature10190

Li, Y., Masitah, A., & Hills, T. T. (2020). The Emotional Recall Task: Juxtaposing recall and recognition-based affect scales. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *46*(9), 1782–1794. https://doi.org/10.1037/xlm0000841

Liao, J., Zhang, B., Xia, W., Cao, Z., Zhang, Y., Liang, S., Hu, K., Xu, S., & Li, Y. (2019). Residential exposure to green space and early childhood neurodevelopment. *Environment International*, *128*, 70–76. https://doi.org/10.1016/j.envint.2019.03.070

Lopes, S., Lima, M., & Silva, K. (2020). Nature can get it out of your mind: The rumination reducing effects of contact with nature and the mediating role of awe and mood. *Journal of Environmental Psychology*, *71*, 1–7. https://doi.org/10.1016/j.jenvp.2020.101489

Mair, P., & Wilcox, R. (2020). Robust statistical methods in R using the WRS2 package. *Behavior Research Methods*, *52*(2), 464–488. https://doi.org/10.3758/s13428-019-01246-w

McCormick, I. A., Walkey, F. H., & Taylor, A. J. W. (1985). The stress arousal checklist: An independent analysis. *Educational and Psychological Measurement*, *45*(1), 143–146. https://doi.org/10.1177/0013164485451013

McMahan, E. A., & Estes, D. (2015). The effect of contact with natural environments on positive and negative affect: A meta-analysis. *The Journal of Positive Psychology*, *10*(6), 507–519. https://doi.org/10.1080/17439760.2014.994224

Miller, R., Stalder, T., Jarczok, M., Almeida, D. M., Badrick, E., Bartels, M., Boomsma, D. I., Coe, C. L., Dekker, M. C. J., Donzella, B., Fischer, J. E., Gunnar, M. R., Kumari, M., Lederbogen, F., Power, C., Ryff, C. D., Subramanian, S. V., Tiemeier, H., Watamura, S. E., & Kirschbaum, C. (2016). The CIRCORT database: Reference ranges and seasonal changes in diurnal salivary cortisol derived from a meta-dataset comprised of 15 field studies. *Psychoneuroendocrinology*, *73*, 16–23. https://doi.org/10.1016/j.psyneuen.2016.07.201

Nolvi, S., Uusitupa, H., Bridgett, D. J., Pesonen, H., Aatsinki, A., Kataja, E., Korja, R., Karlsson, H., & Karlsson, L. (2018). Human milk cortisol concentration predicts experimentally induced infant fear reactivity: Moderation by infant sex. *Developmental Science*, *21*(4), 1–8. https://doi.org/10.1111/desc.12625

Oh, B., Lee, K. J., Zaslawski, C., Yeung, A., Rosenthal, D., Larkey, L., & Back, M. (2017). Health and well-being benefits of spending time in forests: Systematic review.

Environmental Health and Preventive Medicine, *22*(1), 1–11. https://doi.org/10.1186/s12199-017-0677-9

Park, B. J., Tsunetsugu, Y., Kasetani, T., Kagawa, T., & Miyazaki, Y. (2010). The physiological effects of Shinrin-yoku (taking in the forest atmosphere or forest bathing): Evidence from field experiments in 24 forests across Japan. *Environmental Health and Preventive Medicine*, *15*(1), 18–26. https://doi.org/10.1007/s12199-009-0086-9

Park, B.-J., Furuya, K., Kasetani, T., Takayama, N., Kagawa, T., & Miyazaki, Y. (2011). Relationship between psychological responses and physical environments in forest settings. *Landscape and Urban Planning*, *102*(1), 24–32. https://doi.org/10.1016/j.landurbplan.2011.03.005

Park, B.-J., Tsunetsugu, Y., Ishii, H., Furuhashi, S., Hirano, H., Kagawa, T., & Miyazaki, Y. (2008). Physiological effects of Shinrin-yoku (taking in the atmosphere of the forest) in a mixed forest in Shinano Town, Japan. *Scandinavian Journal of Forest Research*, *23*(3), 278–283.

Perkins, S., Searight, H. R., & Ratwik, S. (2011). Walking in a natural winter setting to relieve attention fatigue: A pilot study. *Psychology*, *02*(08), 777–780. https://doi.org/10.4236/psych.2011.28119

Radley, J., Morilak, D., Viau, V., & Campeau, S. (2015). Chronic stress and brain plasticity: Mechanisms underlying adaptive and maladaptive changes and implications for stress-related CNS disorders. *Neuroscience & Biobehavioral Reviews*, *58*, 79–91. https://doi.org/10.1016/j.neubiorev.2015.06.018

Roe, J., Thompson, C., Aspinall, P., Brewer, M., Duff, E., Miller, D., Mitchell, R., & Clow, A. (2013). Green space and stress: Evidence from cortisol measures in deprived urban communities. *International Journal of Environmental Research and Public Health*, *10*(9), 4086–4103. https://doi.org/10.3390/ijerph10094086

Schönbauer, R. (2013). *Das Potential privater Gärten für die wahrgenommene Gesundheit*.

Smyth, J. M., Ockenfels, M. C., Gorin, A. A., Catley, D., Porter, L. S., Kirschbaum, C., Hellhammer, D. H., & Stone, A. A. (1997). Individual differences in the diurnal cycle of cortisol. *Psychoneuroendocrinology*, *22*(2), 89–105. https://doi.org/10.1016/S0306-4530(96)00039-X

Sudimac, S., Sale, V., & Kühn, S. (2022). How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature. *Molecular Psychiatry*, *27*(11), 4446–4452. https://doi.org/10.1038/s41380-022-01720-6

Tekgündüz, S. E., Lazoğlu, M., Nailoğlu, M., Apay, S. E., & Tekgündüz, K. Ş. (2023). The relationship of preterm, term, and post-term births to maternal stress and human milk cortisol levels. *Breastfeeding Medicine*, *18*(6), 462–468. https://doi.org/10.1089/bfm.2023.0006

Tsunetsugu, Y., Park, B.-J., & Miyazaki, Y. (2010). Trends in research related to "Shinrin-yoku" (taking in the forest atmosphere or forest bathing) in Japan. *Environmental Health and Preventive Medicine*, *15*(1), 27–37. https://doi.org/10.1007/s12199-009-0091-z

Tyrväinen, L., Ojala, A., Korpela, K., Lanki, T., Tsunetsugu, Y., & Kagawa, T. (2014). The influence of urban green environments on stress relief measures: A field experiment. *Journal of Environmental Psychology*, *38*, 1–9. https://doi.org/10.1016/j.jenvp.2013.12.005

Veitch, J., Timperio, A., Salmon, J., Hall, S. J., Abbott, G., Flowers, E. P., & Turner, A. I. (2022). Examination of the acute heart rate and salivary cortisol response to a single bout of walking in urban and green environments: A pilot study. *Urban Forestry & Urban Greening*, *74*, 1–8. https://doi.org/10.1016/j.ufug.2022.127660

Vujcic, M., Tomicevic-Dubljevic, J., Grbic, M., Lecic-Tosevski, D., Vukovic, O., & Toskovic, O. (2017). Nature based solution for improving mental health and well-being in urban areas. *Environmental Research*, *158*, 385–392.

Ward Thompson, C., Roe, J., Aspinall, P., Mitchell, R., Clow, A., & Miller, D. (2012). More green space is linked to less stress in deprived communities: Evidence from salivary cortisol patterns. *Landscape and Urban Planning*, *105*(3), 221–229. https://doi.org/10.1016/j.landurbplan.2011.12.015

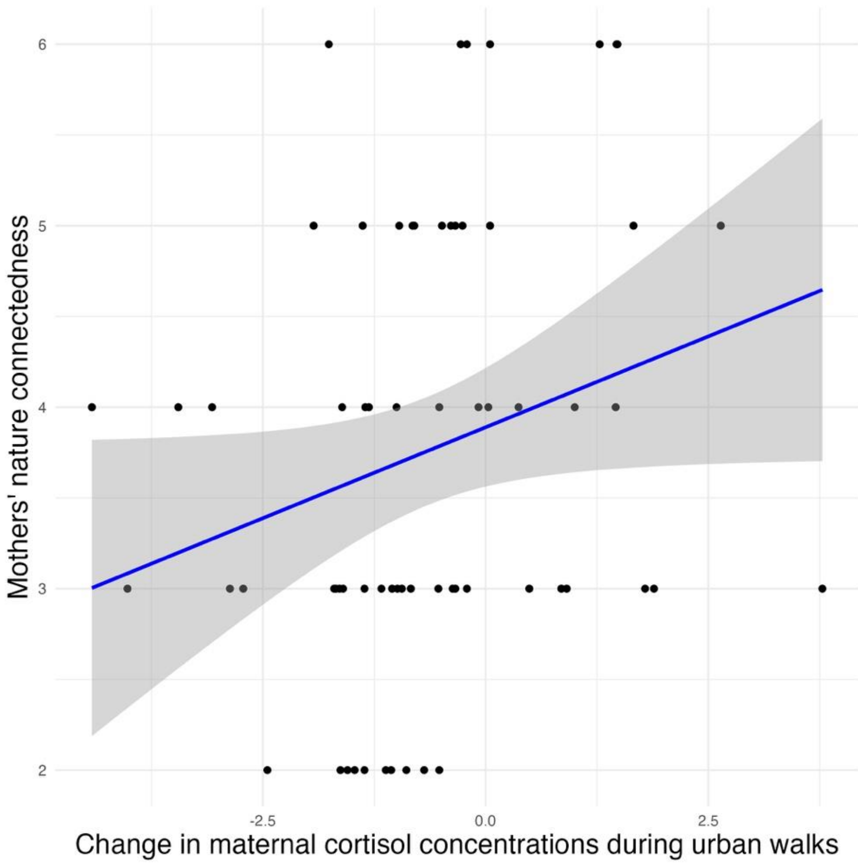
White, M. P., Elliott, L. R., Grellier, J., Economou, T., Bell, S., Bratman, G. N., Cirach, M., Gascon, M., Lima, M. L., Lõhmus, M., Nieuwenhuijsen, M., Ojala, A., Roiko, A., Schultz, P. W., Van Den Bosch, M., & Fleming, L. E. (2021). Associations between green/blue spaces and mental health across 18 countries. *Scientific Reports*, *11*(1), 1–12. https://doi.org/10.1038/s41598-021-87675-0

Supplementary Information

Supplementary results

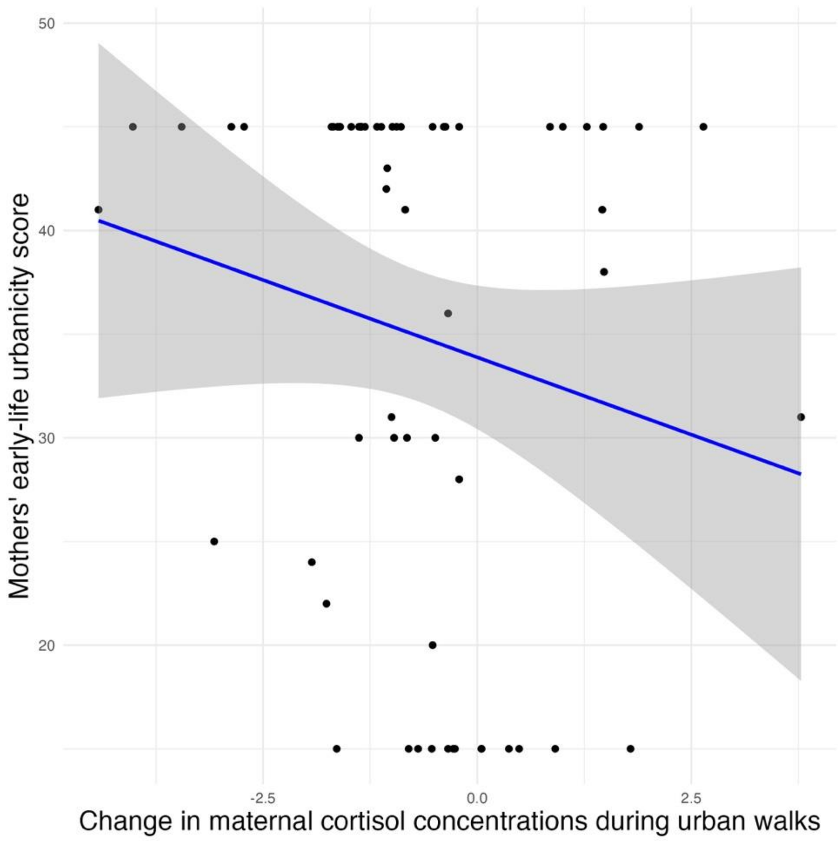
In an exploratory manner, we examined the relationship between changes in cortisol levels during walks with mothers' connectedness to nature, as well as with their upbringing in an urban environment.

In a previous study in which participants went for a walk in an urban and in a natural environment we investigated changes in amygdala activity, a stress-related brain region (Sudimac & Kühn, 2022). This study revealed a positive association between a change in amygdala activity on a social stress task during the urban walk and participants' connectedness to nature only in women, suggesting that women who feel more connected to nature experience a greater impact on their stress-related brain activity during the urban walk. Furthermore, a recent review suggested a mediating effect of connectedness to nature between exposure to natural environments and cortisol concentrations (Gál & Dömötör, 2023). Based on these findings, we exploratorily examined the change in mothers' stress-related salivary cortisol concentrations after the walk (cortisol levels at T1 – T2) with their connectedness to nature. The results revealed a positive correlation between the change in salivary cortisol concentrations during the urban walk and connectedness to nature ($r(62) = 0.30$, $p = 0.01$; Supplementary Figure 1), while no correlation was observed for the walk in nature. This indicates that the greater a mother's connectedness to nature, the higher the increase in cortisol levels during the urban walk. This finding aligns with the previous study showing that women who feel more connected to nature experienced higher change in stress-related amygdala activity during an urban walk (Sudimac & Kühn, 2022).



Supplementary Figure 1. Positive correlation between the change in maternal cortisol concentrations during urban walks and mothers' connectedness to nature

We also observed a negative correlation between a cortisol change during a walk in an urban environment and early-life urbanicity score ($r(62) = -0.27$, $p = 0.037$; Supplementary Figure 2), representing how many years the participant spent in an urban environment or rural environment, until the age of 15 years. This suggests that the more years participants spent in an urban environment during their upbringing, the higher the increase in cortisol levels during a walk in an urban environment. Such correlation was not observed for the walk in a natural environment. This finding parallels a study showing that urban upbringing was associated with increased cortisol levels during acute stress (Steinheuser et al., 2014).



Supplementary Figure 2. Negative correlation between the change in maternal cortisol concentrations during urban walks and mothers' early-life urbanicity score

Overall, these results show that mothers who are highly connected to nature and were brought up in non-urban regions, showed a larger change in cortisol levels during a walk in an urban environment. They suggest that a deep affinity for nature and being brought up in a rural environment may be associated with heightened sensitivity to urban environment and a lower stress threshold, resulting in increased stress-related cortisol production during urban exposure. These results emphasize the need to consider individual differences, like a person's connectedness to nature and their upbringing and current living environments, when examining interactions with urban and natural settings.

References

Gál, V., & Dömötör, Z. (2023). The role of connection with nature in empirical studies with physiological measurements: A systematic literature review. *Biologia Futura*, *74*(3), 281–294. https://doi.org/10.1007/s42977-023-00185-0

Steinheuser, V., Ackermann, K., Schönfeld, P., & Schwabe, L. (2014). Stress and the city: Impact of urban upbringing on the (re) activity of the hypothalamus-pituitary-adrenal axis. *Psychosomatic Medicine*, *76*(9), 678–685. https://doi.org/10.1097/PSY.0000000000000113

Sudimac, S., & Kühn, S. (2022). A one-hour walk in nature reduces amygdala activity in women, but not in men. *Frontiers in Psychology*, *13*, 1–13. https://doi.org/10.3389/fpsyg.2022.931905

E: Declaration of own share

Annex Declaration pursuant to Sec. 7 (3), fourth sentence, of the Doctoral Study Regulations regarding my own share of the submitted scientific or scholarly work that has been published or is intended for publication within the scope of my publication-based work

1. Last name, first name: Sudimac, Sonja
   Institute: Max Planck Institute for Human Development, Berlin
   Doctoral study subject: Psychology
   Title: M.Sc. in Cognitive Science; M.Sc. in Educational Psychology; B.A. in Psychology

2. **Numbered listing of works submitted (title, authors, where and when published and/or submitted):**

   1. **Sudimac, S.**, Sale, V., & Kühn, S. (2022). How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature. *Molecular Psychiatry*, *27*(11), 4446-4452. doi: 10.1038/s41380-022-01720-6

   2. **Sudimac, S.**, & Kühn, S. (2022). A one-hour walk in nature reduces amygdala activity in women, but not in men. *Frontiers in Psychology*, *13*, 1–13. doi: 10.3389/fpsyg.2022.931905

   3. **Sudimac, S.**, & Kühn, S. Can a nature walk change your brain? Investigating hippocampal brain plasticity after one hour in a forest. (submitted 2024)

   4. **Sudimac, S.**, Drewelies, J., De Weerth C.* & Kühn, S.* Effects of a walk in a residential natural vs. urban environment on objective and subjective stress indicators in mothers and their infants. (submitted 2024)
      * These authors share last authorship.

3. **Explanation of own share of these works:**

   The amount of the work completed by myself is evaluated on the following scale:
   all – the vast majority – most – part.

Regarding 2.1.: experiment design (most), method development (the vast majority), data collection (all), data analysis and programming (the vast majority), data visualization (all), interpretation and discussion of results (the vast majority), preparing the manuscript (all).

Regarding 2.2.: experiment design (the vast majority), method development (the vast majority), data collection (all), data analysis and programming (all), data visualization (all), interpretation and discussion of results (the vast majority), preparing the manuscript (all).
Regarding 2.3.: experiment design (part), method development (most), data collection (all), data analysis and programming (the vast majority), data visualization (all), interpretation and discussion of results (the vast majority), preparing the manuscript (all).

Regarding 2.4.: experiment design (most), method development (the vast majority), data collection (all), data analysis and programming (the vast majority), data visualization (all), interpretation and discussion of results (the vast majority), preparing the manuscript (all).

4. Names and e-mail addresses for the relevant co-authors:

Regarding 2.1.: Vera Sale (vera.sale18@gmail.com),
Simone Kühn (kuehn@mpibberlin.mpg.de)

Regarding 2.2: Simone Kühn (see above)

Regarding 2.3: Simone Kühn (see above)

Regarding 2.4: Johanna Drewelies (drewelies@mpib-berlin.mpg.de),
Carolina de Weerth (Carolina.deWeerth@radboudumc.nl),
Simone Kühn (see above)

Berlin, January 2024,

Sonja Sudimac

F: Declaration of independent work

I hereby declare that:

- I have written this dissertation independently and without unauthorized assistance,
- I have not submitted this dissertation to any other university and that I do not hold a doctoral degree in the subject of psychology, and that
- I am aware of the doctoral regulations for the degree of Dr.rer.nat. / Ph.D. in the Department of Education and Psychology at the Freie Universität Berlin, as amended on August 8th 2016.

Berlin, January 2024

Sonja Sudimac

G: Curriculum Vitae

Sonja Sudimac
Max Planck Institute for Human Development
Lentzeallee 94, 14195 Berlin

Education & Training

11/2019 – Present	Free University of Berlin, Berlin, Germany Doctoral Student
04/2020 – Present	International Max Planck Research School on the Life Course (LIFE) Fellow
10/2016 – 01/2019	Technical University of Kaiserslautern, Kaiserslautern, Germany MSc Cognitive Science (grade: 1.0/first) Supported by DAAD Scholarship Master's thesis: Neural correlates of social exclusion by own child in fathers: is there an association with attachment style?
10/2015 – 09/2016	University of Belgrade, Belgrade, Serbia MSc Educational Psychology (grade 9.3/10) Master's thesis: Parental perceptions of socio-emotional responsiveness of children with autism spectrum disorder and children's impact on the family as factors of parental stress
10/2011 – 07/2015	University of Belgrade, Belgrade, Serbia BSc Psychology (grade 8.7/10)
09/2013 – 07/2014	University of Granada, Granada, Spain Visiting Student supported by Erasmus Mundus scholarship

Research positions

07/2019 – Present	Pre-Doctoral Fellow, Lise Meitner Group for Environmental Neuroscience, Max Planck Institute for Human Development, Berlin, Germany
06/2018 – 03/2019	Research Intern and Guest Researcher, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
10/2017 – 03/2018	Research assistant at the Department of Cognitive Neuroscience, Technical University of Kaiserslautern, Kaiserslautern, Germany
01/2014 – 06/2014	Intern, Brain House Institute, Granada, Spain

Publications

Journal Articles

2023 Cabiró P. M., **Sudimac, S.**, Stobbe E., Kühn S. (2023). Urbanization is positively associated with global perceptual style. *Journal of Environmental Psychology*, *91*, 1–10. https://doi.org/10.1016/j.jenvp.2023.102100

2023 Eyre, H. A., Ibáñez, A., Falcao, V. P., Winter, S. F., Berk, M., Gilbert, B. J.,(...) **Sudimac, S.**,(...) Salama M. (2023). Brain capital is key to a sustainable future. *Rice University's Baker Institute for Public Policy*. 1–44. https://doi.org/10.25613/5yez-tc65

2022 **Sudimac, S.**, Sale, V., Kühn, S. (2022). How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature. *Molecular Psychiatry, 27*(11), 4446–4452. https://doi.org/10.1038/s41380-022-01720-6

2022 **Sudimac, S.**, Kühn S. (2022). A one-hour walk in nature reduces amygdala activity in women, but not in men. *Frontiers in Psychology, 13*, 1–13. https://doi.org/10.3389/fpsyg.2022.931905

2022 Sztuka, I.M., Örken, A., **Sudimac, S.**, Kühn, S. (2022). The other blue: Role of the sky in the perception of nature. *Frontiers in Psychology*, *13*, 1–16. https://doi.org/10.3389/fpsyg.2022.932507

2021 Tawil, N., Sztuka, I.M., Pohlmann, K., **Sudimac S.**, Kühn S. (2021). The Living Space: Psychological Well-Being and Mental Health in Response to Interiors Presented in Virtual Reality. *International Journal of Environmental Research and Public Health*. *18*(23), 1–20. https://doi.org/10.3390/ijerph182312510

Preprints

2024 **Sudimac, S.**, & Kühn, S. *Can a nature walk change your brain? Investigating hippocampal brain plasticity after one hour in a forest.* PsyArXiv. https://doi.org/10.31234/osf.io/g64bq
[Manuscript under revision]

2024 **Sudimac, S.**, Drewelies, J., De Weerth C.* & Kühn, S.* *Effects of a walk in a residential natural vs. urban environment on objective and subjective stress indicators in mothers and their infants.* PsyArXiv. https://doi.org/10.31234/osf.io/pz83m
[Manuscript under revision]
* These authors share last authorship.

Book chapters

In press	Beyer M., **Sudimac, S.**, Steininger M. & Kühn, S. (in press). Interplay between the physical environment and the human brain: Insights from MRI research. In S. Kühn (Ed.), *Environmental Neuroscience*. Springer.

Invited talks

01/2024	Technical University of Dresden, Germany *How does nature affect the brain and mental health? Perspectives from Environmental Neuroscience*
11/2022	Leuphana University of Lüneburg, Germany *How does the environment shape the brain? Introduction to Environmental Neuroscience.*

Conferences

Oral presentations

06/2023	International Conference on Environmental Psychology, Aarhus, Denmark *Does the nature change your brain? A walk in nature induces hippocampal structural brain plasticity* Chair of the symposium *Environmental Neuroscience*: *An emerging field investigating human-environment interactions*
05/2023	Association for Psychological Science, Washington D.C., USA. *How does a walk in nature impact the brain: Exploring the neural mechanisms behind nurturing effects of nature*
07/2022	European Society for Cognitive and Affective Neuroscience, Vienna, Austria *How nature nurtures: Amygdala activity decreases as the result of a one-hour walk in nature*
10/2021	International Conference on Environmental Psychology, Syracuse, Italy *Where to go for a walk? Investigating neural consequences of a one-hour walk in natural vs. urban environment*

Poster presentations

07/2023	International Society for Developmental Psychobiology, Utrecht, The Netherlands *Effects of a walk in a natural vs. an urban environment on stress in mothers and their infants*

Funding

10/2023	Max Planck Dahlem Campus of Cognition, Cross-group collaboration (550 euros for participants remuneration) Project *Umwelt-COMIC: Investigating environmental exposure in childhood brain and memory development*

Advising

Undergraduate & Postgraduate students

Jennifer DiMascio-Donohue**, Elena Isenberg**, Jordan Elias**, Marina Picó Cabiró**, Ada Örken**, Jakob Firnrohr**, Vera Sale**, Sonali Beckmann*, Kim Falkenstein, Alessandra Braci, Hannah Kruft, Mirjam Reidick

*Bachelor thesis mentee, **Master's thesis mentee