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Special Feature: Wildlife behaviour and movement ecology in a human-dominated world. Guest edited by Michael G. Bertram, Jack A. Brand and Marlee A. Tucker.

Wildlife movement responses to the  
press–pulse–pause of the Anthropocene

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Wildlife is increasingly forced to share space with humans, facing disturbances that operate across different spatial and temporal scales. The press–pulse framework, originally developed in the disturbance ecology literature, distinguishes between long-term sustained ‘presses’ and more acute ‘pulses’. Because pulses occur during ongoing press conditions, their ecological effects depend on how they interact with that background, helping explain why certain disturbances result in transient, localized changes, while others lead to lasting, widespread impacts. Here, we expand this framework by applying it to regimes of human disturbances, and incorporating ‘pauses’ as a third category. Pulses and pauses (e.g. episodes of extreme weather, or drastic changes in human mobility) can substantially affect wildlife behaviour, yet their effects are often modulated by background ‘press’ conditions. We offer a conceptual framework for disentangling effects across space and time and highlight how plasticity in wildlife movement—particularly in terms of navigating risks and tracking resources—can lead to both adaptive and nonadaptive responses to human disturbances. This enables predictions about how shifts in animal movement can influence human wildlife interactions and conflict with humans under different scenarios. Applying the press–pulse–pause framework to movement ecology allows researchers to improve our understanding of how wildlife is affected by different disturbance regimes, advancing efforts to foster sustainable human–wildlife coexistence in an era of mounting pressures.

## 1. Introduction

Biodiversity worldwide is principally threatened by human disturbances. With over 70% of the world’s land surface substantially altered and the global overlap of humans and wildlife expanding [1], anthropogenic disturbances present an existential risk to species’ persistence. Human activities include a broad range of anthropogenic factors, including static infrastructure such as roads, fences and buildings, as well as dynamic human movement and transportation, and associated byproducts, including artificial light at night, noise pollution [2,3] and greenhouse-gas emissions. These disturbances occur over varying timescales—some sustained, others abrupt—profoundly impacting individual-level phenotypic traits and fitness outcomes, leading to restructuring of wildlife populations and communities [4–6]. Such disturbances have driven unprecedented extinction rates, further undermining ecosystem function and stability and jeopardizing human health and wellbeing [7–9]. These drivers constitute human-induced rapid environmental changes, whereby human disturbances alter ecological

conditions on timescales that can outpace organisms' behavioural, physiological or evolutionary responses [10]. These disturbances are intensifying and becoming less predictable in the Anthropocene; a period in which human activity has become a dominant force shaping Earth's climate, landscapes and ecological processes [11], altering the conditions under which biodiversity must persist alongside humans. Hence, the interacting consequences of human disturbances on biodiversity necessitate a more comprehensive framework for understanding how ecological responses emerge across space and time. Simultaneously, determining wildlife responses across multiple human disturbances is appropriate for bolstering adaptive management solutions to mitigate future conflicts.

The press–pulse framework, which was first established in the ecological disturbance literature [12–14], may be particularly appropriate for explaining how spatiotemporal variability in human disturbances is associated with specific wildlife responses. Briefly, this framework distinguishes press disturbances as events that have sustained and gradual impacts with often long-term consequences, from pulse disturbances as abrupt, acute events that typically elicit immediate responses, and can be repetitive or singular [12]. The framework has been applied across diverse disturbance contexts, including community perturbation experiments, ecosystem dynamics, resource pulses, fire ecology and climate variability [12,15–18]. In global change biology research, presses represent gradual shifts in the mean or variance of climatic factors (e.g. mean annual air temperature or sea ice thickness), and pulses refer to more acute events (e.g. cold snaps, droughts or heatwaves) [16]. We note that these categories are scale-dependent. For example, drought may be treated as a pulse relative to multi-decadal climatic change, but as a press when biological responses are measured over shorter ecological or organismal timescales. Thus, press, pulse and pause events should be defined relative to the temporal baseline and response variable under study.

Although most studies consider presses or pulses in isolation, a key strength of the press–pulse framework is its emphasis on the potential for these phenomena to co-occur and interact. For instance, a 38-year study of Magellanic penguins demonstrated how marine heatwaves (pulses) negatively affected adult survival, whereas long-term increases in sea surface temperatures and declining productivity (presses) harmed both juveniles and adults, which taken together, contributed to population decline [15]. Thus, failing to account for one disturbance may mask critical biological impacts of the other, hindering our understanding of how overlapping disturbances affect wildlife [15]. These insights can extend to investigating the combined effect of human disturbances, where multiple press and pulse disturbances co-occur. By explicitly integrating multiple disturbance types into a coherent, unified approach, the press–pulse framework offers a promising opportunity to advance ecological research, enabling more effective predictions to address complex human–wildlife interactions across diverse contexts.

While research using the press–pulse framework has often focused on phenological and distributional changes [16], behavioural responses may warrant further attention. Behavioural traits may be especially insightful in the press–pulse framework. Behaviours are often labile, highly sensitive to environmental perturbations, and affect both interspecific and intraspecific interactions, which fundamentally shape population and community dynamics [19,20]. Behaviour also represents organisms' 'first response' to environmental stressors, enabling coping strategies that, if effective, positively affect fitness [21]. A key mechanism underlying these responses is behavioural plasticity, defined as the capacity of individuals to adjust their behaviour in response to changing environmental conditions [22]. Thus, wildlife behaviours can serve as a sensitive signal of impact [10,23,24]. Human disturbance principally alters wildlife's exposure to risks (e.g. predation hazards) and resources (e.g. food availability, habitat quality), which in turn dictates how animals use and navigate spaces to balance resource acquisition against the risk of injury or death [12]. As a result, the magnitude and frequency of human disturbances may exert strong selection for specific behavioural phenotypes [25], while also constraining animal's capacity to adjust behaviour to local conditions [10]. Together, these processes may increase unpredictability in trait expression over time [5]. Accordingly, human disturbances may reduce intraspecific behavioural differences among individuals within a population, even as those same disturbances require animals to flexibly adjust their behaviour to current conditions. However, the extent of this plasticity is likely to depend on environment context and species life history traits [26].

Animal movement is an especially promising suite of behavioural traits for illustrating the utility of a press–pulse framework for human disturbances [27,28]. First, a well-established and growing literature has repeatedly described how human disturbance alters the movement patterns of a variety of vertebrate taxa across the globe [29,30]. Second, advances in recognizing the importance of behavioural states, among-individual differences (i.e. personality), and within-individual consistency (i.e. repeatability) [31–33], has transformed the hypotheses we can address. Advances in movement ecology enable exploration of behavioural traits, potentially associated with the press or pulse of human disturbances [28,34–36]. Third, with new tracking technologies and analytical approaches, researchers can gather fine-scale information about the movements of individual animals over long timescales and across entire species' ranges [34,35,37], facilitating insights into wildlife behaviour before, during and after pulse disturbances [36]. In parallel, progress in cloud-based geospatial platforms (e.g. NASA DAAC, Google Earth Engine, Microsoft Planetary Computer) has facilitated the annotation of dynamic and static remote sensing information in unprecedented ways [38,39], enabling movement ecology studies that more accurately assess behavioural responses to environmental perturbations.

In this perspective, we first extend the press–pulse framework beyond its prior application in ecological disturbance and climate change research to the broader domain of human disturbances. Second, we incorporate a third category, 'pauses' (e.g. reductions in human mobility during COVID-19 lockdowns), to better understand animal movement responses. There is tremendous variation in how wildlife responds to presses, pulses and pauses [30,40–44], highlighting the need to understand the spatio-temporal dynamics and interplay of these processes. We begin by providing a brief summary of the press–pulse framework, its component parts, and how it captures temporal dynamics. Second, by connecting the press–pulse–pause framework with movement ecology, we show how multiple human disturbances interactively influence behaviour (e.g. risk-taking and resource tracking), highlighting an important role for behavioural plasticity. Third, we discuss how wildlife responses emerge from interacting disturbance regimes, where background press conditions can modulate responses to pulses

and pauses. By linking these disturbance types to measurable behavioural responses, this framework provides a foundation for generating predictions under overlapping anthropogenic pressures. Specifically, behavioural responses to pulses and pauses are expected to depend on background press intensity, with stronger or more variable responses in areas with low press intensity than in areas with high press intensity, where responses may be more constrained. However, pulse disturbances may also elicit stronger responses in high-press areas when they interact synergistically with existing anthropogenic pressures. Moreover, this framework can also inform empirical study design by providing a holistic perspective on anthropogenic pressures and their biological consequences. We conclude by discussing the applicability of this framework to anticipating human–wildlife overlap and potential conflicts that can jeopardize biodiversity conservation. We draw primarily on case studies of movement ecology and their responses to human disturbances.

## 2. Temporal dynamics of human disturbances: anthropogenic presses, pulses and pauses

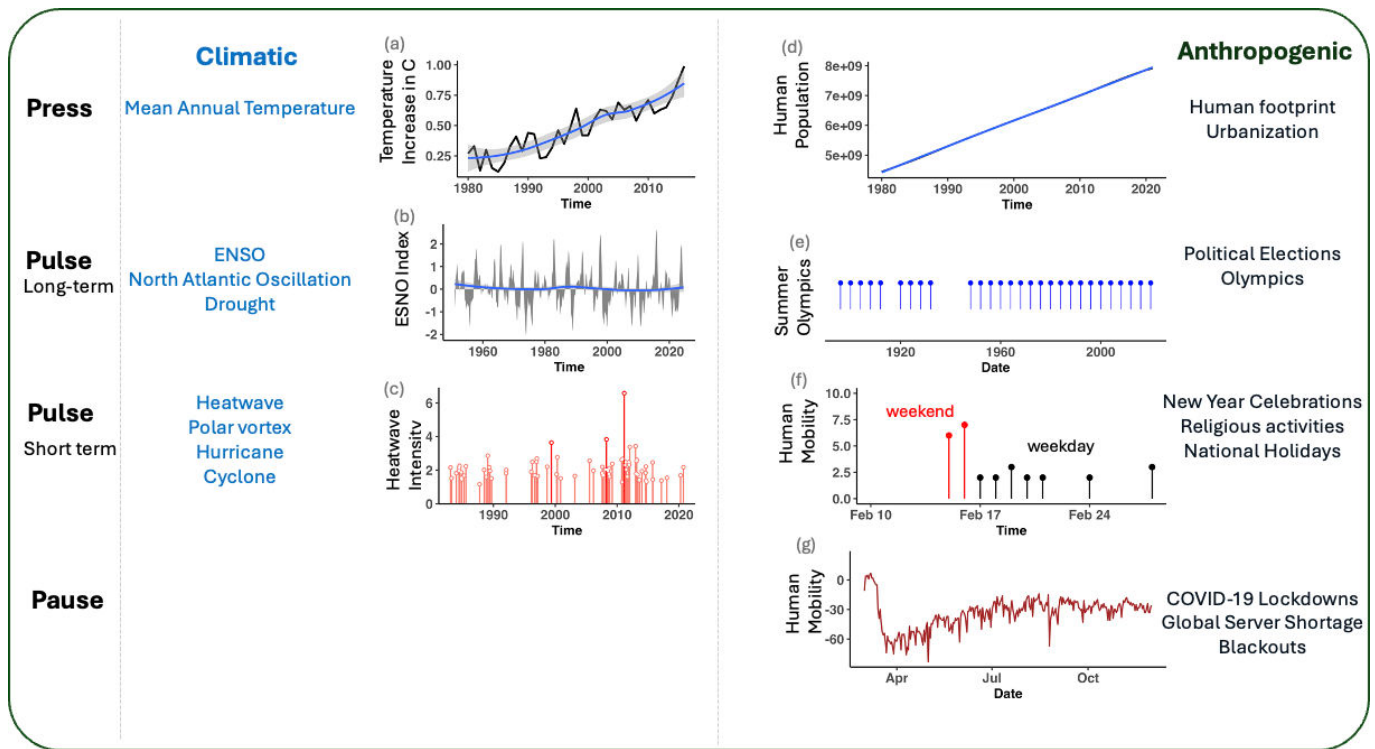
Worldwide, the human footprint—the aggregation of infrastructure, and population density, commonly quantified using the Human Footprint Index—has seen a sustained and consistent increase over the past decades, despite substantial regional variation in the rate of change [45]. This cumulative expansion represents a dominant press of human disturbances [45–47] (figure 1). As its intensity increases, mammals are moving shorter distances, over varying timescales, highlighting how gradual, pervasive human impacts can alter wildlife behaviour [29]. In the case of brown bears (*Ursus arctos*), an increasing human footprint index has led individuals to display lower daily displacements and long distance movements, as well as smaller home ranges [48].

Some human disturbances are repetitive (figure 1), such as cultural events, which can shift travel and disturbance patterns. For example, New Year's fireworks across Denmark, Germany and the Netherlands led four geese species to fly longer distances at higher altitudes. This immediate behavioural adjustment in risk-exposure appeared to be followed by individuals moving less and subsequently increasing their foraging time, likely to compensate for this increased energy expenditure for several days after the initial disturbance [49]. This example illustrates how anthropogenic pulses can induce temporary, but substantial, behavioural responses in wildlife. In addition to presses and pulses, periods of reduced human mobility or pauses, may offer complementary insights into human–wildlife interactions [3,50]. The COVID-19 pandemic provided a quasi-experimental perturbation for researchers to study animal behaviour in response to sudden declines of human mobility (although spikes of human mobility were observed locally, as governments allowed some forms of recreation) [50]. A recently introduced classification scheme defines an 'anthropause' as an extreme case of a human pause, in terms of magnitude and spatial extent [3]. Examples of shorter-term pauses include events like power blackouts or software malfunctions, which may temporarily halt human transport at local or regional scales (figure 1). Moreover, armed conflicts, with their wide-ranging anthropogenic impacts, can simultaneously act as pulses and presses, altering typical human activity and disturbance patterns [51,52].

When characterizing press–pulse–pause events, it is important to consider multiple axes that may determine impacts on wildlife behaviour: this includes their magnitude, spatial extent and duration, as well as additional factors, including onset and frequency [16]. Magnitude refers to the overall intensity of the event (and in our framework can be measured in different units), ranging from slight perturbations (e.g. gradual noise increases) to catastrophic shifts (e.g. drastic habitat loss). The spatial scale determines whether the disturbance is localized (e.g. a local regional infrastructure failure) or more widespread (e.g. continental-scale public health emergency measures, including COVID-19 lockdowns) (figure 2). In the case of our previous Magellanic penguin example, the frequency of the climatic pulse appeared to have a larger impact than the magnitude of the event [15]. Duration distinguishes pulses (e.g. holiday fireworks) from more sustained press events (e.g. continual urban expansion). Frequency captures how often an event occurs, including sporadic (e.g. power blackouts) or cyclical (e.g. annual celebrations) patterns. For instance, wildlife may be more likely to rapidly adjust their behaviour to predictable or recurrent seasonal pulses. Onset can be abrupt or gradual, which may influence whether organisms can respond to a change. Another important aspect is the autocorrelation of these events, that is, how the timing of one pulse relates to another (see [53,54] for theoretical example on extreme heatwaves). Closely spaced or overlapping pulses can create compounding effects before individuals and populations recover from an initial disturbance [53]. Conversely, longer intervals between disturbances may allow time for behavioural adaptation or habitat recovery, potentially dampening overall impacts. Exploring these complex interactions holds the potential to reveal why some disturbances result in transient, localized behavioural shifts while others produce long-lasting, wide-ranging ecological outcomes.

To illustrate how the press–pulse–pause framework can be operationalized for movement ecology, we present a conceptual example based on the 2026 FIFA World Cup as a scheduled anthropogenic pulse. First, we identify the spatial footprint of the host metropolitan regions across Mexico, Canada and the United States, intersect these regions with the deployment centroids of animal movement studies in the Movebank database, and retain only those that overlap with the year 2026 [55]. Because additional datasets exist outside Movebank, we also include coyotes (*Canis latrans*) in this example, given known planned tracking efforts in the San Francisco–Oakland–Fremont metropolitan area in California. Data owners could then be approached with hypotheses grounded in press–pulse–pause dynamics, enabling coordination of study designs around scheduled disturbances before these events occur (*sensu* [3]).

Where possible, distinguishing pulse and pause effects will benefit from pairing analyses with baseline movement data. This requires structured study designs, including before–during–after comparisons or replicated gradients of press intensity, to reduce spatial confounding [56]. For example, repeated measures of individual animals during COVID-19 lockdowns and corresponding periods in the previous year showed that weekly changes in the space use of terrestrial birds and mammals across the United States were partly attributable to behavioural plasticity within individuals [57]. This study illustrates how



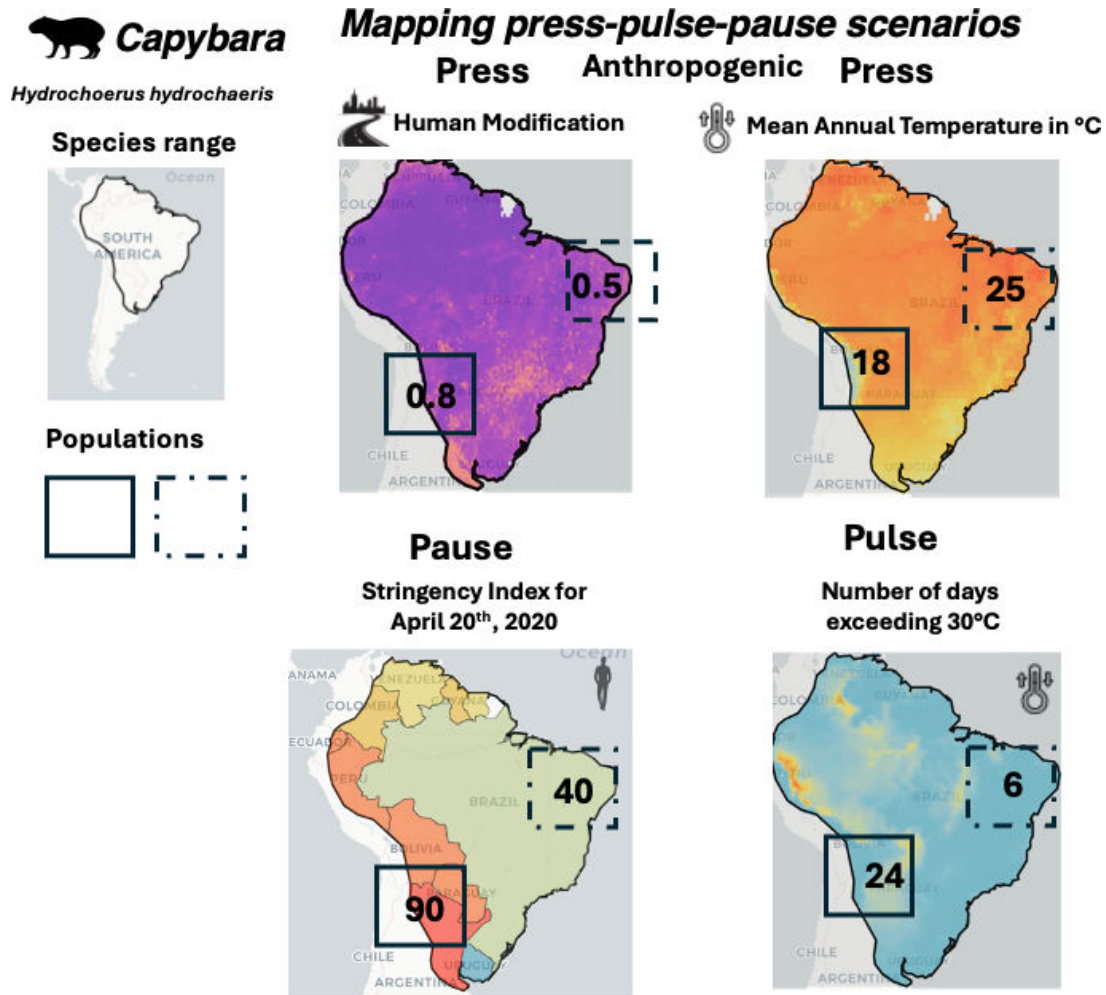
**Figure 1.** Examples of press, pulse and pause dynamics across anthropogenic and climatic disturbances. While a press may represent a sustained increase, pauses and pulses can occur at shorter intervals and vary in magnitude and frequency. (a) Consistent increase in mean annual temperature at the global scale is a press. (b) The El Niño and Niña Southern Oscillation (ENSO) represents long-term climatic anomalies with substantial impacts on the world climate. El Niño and La Niña events can be considered a pulse occurring at varying frequencies. Drought is shown here as a long-term pulse relative to longer climatic baselines, although it may function as a press when responses are measured over shorter ecological or organismal timescales. (c) Marine heatwaves represent a pulse, and are often of short duration with strong magnitude. (d) Anthropogenic presses include sustained processes such as urbanization and the long-term expansion of human infrastructure, often measured through the human footprint index. (e) Events such as Olympics or festivals, can be of strong magnitude, i.e. substantial increases in human activity, and represent anthropogenic pulses that are recurring. (f) Regular increases in human mobility, such as weekend spikes in urban greenspace use, are also examples of anthropogenic pulses. (g) Reductions of human mobility across large spatial extents and of large magnitude, such as those induced by COVID-19 lockdowns, city-wide blackouts or global server shortages reducing aviation traffic, represent pauses.

evaluating whether behavioural responses persist or reverse in relation to underlying press conditions can help disentangle transient pulse or pause effects from longer-term press-mediated changes. Where pre-event baselines are unavailable, space-for-time substitutions or multi-year baselines can provide alternative options for ecological inference [3]. Although such control conditions are not always available, the growing number of long-term animal telemetry datasets makes it increasingly feasible to identify suitable studies retrospectively [55,58,59]. These datasets also enable prospective study design around scheduled disturbance events, as well as analysis of past pulse or pause events.

### 3. Behavioural plasticity in risk responses and resource tracking

Behavioural plasticity (i.e. within-individual plasticity) refers to the capacity of individual animals to adjust their behaviour in response to changing conditions or disturbances, which can involve rapid adjustments that may be reversible, potentially offering resilience in dynamic human-altered environments [22]. Movement data are particularly well suited for assessing how animals respond to both gradual and sudden anthropogenic disturbances. This is facilitated by improvements in the near-real-time transfer of tracking data, and the identification of behaviours through on-board sensors, such as accelerometers and advanced behavioural classification methods [28,34]. For example, the increased sophistication of hidden Markov models and behavioural change point analysis approaches facilitate the identification of specific behavioural responses (e.g. foraging, resting, moving, daily activity budgets) that are likely to shift under a particular combination of human disturbances (e.g. altered movement patterns in response to a spike in human recreation) [60–62]. Comparative analyses of movement-based habitat selection across 48 terrestrial mammal species, using step-selection functions, showed that responses to human disturbance are highly plastic within species and shaped by disturbance context, including roads and human population density—core components of the human footprint index [63]. This context-dependent variation highlights that behavioural responses to human disturbance can vary substantially within species, not only among species [63].

However, behavioural plasticity can become maladaptive, particularly when it appears to limit or slow down physiological adaptation to changing conditions [64], or results in ineffective responses to novel disturbances. In contrast, species habituated to press conditions may exhibit limited behavioural plasticity and struggle to adjust with abrupt pulses or press conditions that exceed a certain threshold, leading to maladaptive behaviours that jeopardize fitness [65]. For example, behaviours such as site fidelity—historically adaptive in stable environments—can become maladaptive under rapid anthropogenic change,



**Figure 2.** Press, pulse and pause conditions vary across populations. Anthropogenic and climatic presses, pulses and pauses are mapped across the geographic range of capybaras (*Hydrochoerus hydrochaeris*) in South America to illustrate spatial variation in disturbance regimes and identify populations suitable for designing comparative movement ecology studies. These spatial contrasts are intended to illustrate variation in disturbance regimes rather than serve as direct experimental comparisons. For example, capybaras in areas with high human-modification may exhibit pronounced home-range contractions and heightened nocturnal activity during acute pulses such as extreme heat events. Values within each square represent press–pulse–pause metrics for two different regions. The left square represents higher human development (e.g. Human Footprint Index = 0.8) and stricter COVID-19 lockdowns (Oxford COVID-19 Government Response Stringency Index = 90, on a 0–100 scale where higher values indicate stricter restrictions). Simultaneously, each of these two areas have substantially different mean temperatures as well as substantial differences in the number of pulses in the form of extreme heat (total of 24 days exceeding 30°C a year versus 6 days).

as individuals persist in previously suitable but now degraded habitats [66]. Importantly, reversibility of behavioural change—how quickly animals return to their pre-disturbance behavioural state following a pause or pulse event—can vary substantially across individuals and appears to further depend on the magnitude of the disruption and the context of preceding press conditions [16].

Diagnosing the tipping points that trigger behavioural shifts, induce plasticity or solicit reversibility are critical for conservation efforts, particularly when faced with rapid anthropogenic climate [67] or induced evolutionary change [22,68]. Behavioural plasticity can include variation in *risk responses*, including changes of diurnal activity patterns as a trade-off between threat exposure and the need for resource gain or thermoregulation; and *resource tracking*, manifested in the predictability of resource selection by wildlife on the move [69–71] (figure 3). The press–pulse–pause framework may also prove insightful in determining the permissibility of certain behavioural types under various disturbance regimes. Consistent or among-individual differences in behavioural traits (i.e. animal personality, behavioural phenotypes, etc.) including boldness, exploration or risk tolerance derived from movement metrics (e.g. displacement, habitat selection) can enable the estimation of behavioural phenotypes as a function of press–pulse–pause gradients [31,72]. For instance, low repeatability and relatively homogeneous responses to certain pulses or presses (e.g. recreational activity or urbanization) may indicate all individuals in a population conform their behaviour to a narrowly defined optimum to increase their fitness, regardless of personality differences. By contrast, reductions in human disturbance may permit greater variability in behavioural trait expression without selective disadvantages. Quantifying individual variation in behavioural predictability can additionally reveal which disturbance types induce greater unpredictability in behavioural traits [32]. Further still, correlations among movement-derived behavioural traits (i.e. behavioural syndromes) may enable us to test whether press–pulse–pause events decouple or intensify trait linkages [73]. In sum, the press–pulse–pause framework provides an exciting new frontier in both animal personality and movement ecology that can generate new empirical approaches that directly assess how disturbance regimes facilitate or inhibit among- and within-individual variation in behaviour.

## (a) Risk responses

Perceived risk is an important driver of animal behaviour and movement, as animals must balance risk avoidance with resource acquisition and other fitness-relevant activities, navigating a dynamic 'landscape of fear' [74,75]. Human disturbance can modify risk for animals in many ways [69], from instilling fear in animals [75], to reducing or eliminating predation pressures [76]. Changes in human mobility (e.g. recreation or road traffic), or its byproducts in the form of noise or artificial light at night, can result in pulses of perceived risk for animals, particularly for large mammalian predators [75,77,78]. Predators can change their behaviour in various ways in response to perceived risk from humans, including a behavioural shift towards nocturnal activity to reduce daytime encounters with humans, representing a response to a daily disturbance pulse [70,79]. On the other hand, some herbivore prey seek refuge in human-dominated areas to evade natural predators, leveraging humans as a 'shield' to reduce predation risk [76], and so may be responsive to press dynamics, including urban expansion.

In our press–pulse–pause framework, the long-term intensity of human landscape modification sets a baseline 'landscape of fear', while short-term pulses or pauses can increase or decrease that perceived anthropogenic risk, leading to corresponding movement shifts. Repeated exposure to the press of benign human activity may habituate animals to human presence and thus reduce risk perception associated with pulses. A study analysing data from 42 terrestrial mammal species that had been followed with tracking devices revealed that individuals captured in highly disturbed landscapes recovered to baseline movement patterns quicker than those in more remote regions [80]. This pattern suggests greater habituation to anthropogenic risk and faster recovery from human disturbance. Capture for tagging may constitute an acute traumatic point-event, rather than an anthropogenic pulse as conceptualized in our framework. Together, these results point to a likely interaction of long-term and short-term impacts, suggesting that background press conditions modulate responses to short-term disturbances [80]. During the COVID-19 anthropause, many terrestrial mammals across the world exhibited changes in their activity budgets and nocturnal behaviour, and the intensity of these responses appeared to be associated not only with the degree of reduced human mobility (pause) but also with the degree of human landscape modification (the background anthropogenic press) [81] (figure 4a). Taken together, these findings indicate that mapping individual differences in risk-taking means and variance can improve our capacity to model and predict the behavioural responses of wildlife to future changes in human activity [6,88].

In human-modified landscapes, mammals can exhibit reduced daily movement, likely as a strategy to avoid direct human encounters or due to constraints imposed by human infrastructure [29]. At a local scale, radio-collared mountain lions (*Puma concolor*) in Santa Cruz, California, increased their affinity towards urban areas during the COVID-19 anthropause, suggesting a shift in space use [82]. Moreover, mountain lions in another far more intensively urbanized part of California (in and around Los Angeles) appeared to reduce their overall movements, thus optimizing their energy expenditure, highlighting rapid behavioural adjustment to a pause event [89]. In Canada, a decline in recreational heli-skiing led to 80–120% increases in the home range sizes of collared caribou (*Rangifer tarandus*) [85]. These results indicate that the overall negative effect of human landscape modification can be temporarily relieved by the effect of a major human pause (figure 4). The extent of these responses underscores how species navigate the interplay of press, pulse and pause dynamics, adjusting their space use to balance risk avoidance with resource acquisition. Home ranges, diurnal patterns and the response to human infrastructure can all shift in either direction in response to altered risk regimes or resource availability.

## (b) Resource tracking

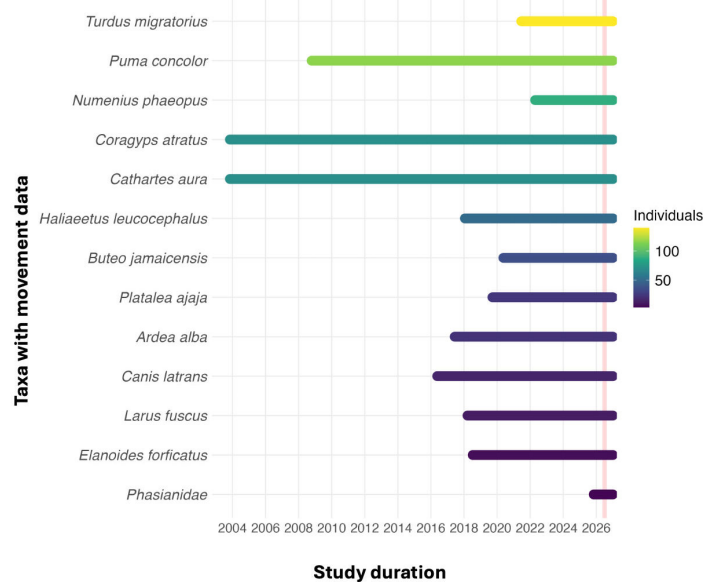
Resource tracking refers to animals adjusting their movements to follow phenological variation in key resources, shaping movement strategies and energetic gains in heterogeneous environments [71]. Understanding the degree to which animals track resources can help predict the impacts of anthropogenic presses, pulses and pauses, for example, when they create barriers to animal movement. Sustained pressures such as energy infrastructure developments, can disrupt the ordered progression of resources across a landscape ('resource waves') that animals frequently track during migration (figure 4). For instance, while mule deer (*Odocoileus hemionus*) typically adjust their migratory routes to track the spring green-up of vegetation, the long-term development of industrial gas fields forced their movements to stall at the edges of migratory corridors, reducing optimal tracking by approximately 39% and compromising the persistence of migratory corridors [83]. To date, research on large herbivores and whales has highlighted how long-lived animals may track long-term trends more strongly than annual optima in foraging resources [90,91]. That said, substantial behavioural plasticity in resource tracking strategies have been observed within species, populations and individuals. For example, whooping cranes (*Grus americana*) have been shown to improve their resource tracking ability as they age, increasingly synchronizing their migration with peak vegetation phenology over successive years, demonstrating within-individual behavioural plasticity in resource tracking [92].

There may be multiple strategies of resource tracking across individuals, of which some may be adaptive by relating movement to predictable resource dynamics, and others maladaptive as background press conditions become increasingly variable and less predictable. Migratory ungulates that track the progression of resource phenology ('green-wave surfing') can increase body condition and fitness by closely matching peak resource availability [93]. Across realms, resource tracking itself may become maladaptive when reliance on historically stable environmental cues leads to mismatches with current conditions. In the oceans, blue whales (*Balaenoptera musculus*) appear to track long-term average resource conditions, using memory to target historically productive foraging areas [90]. While advantageous in predictable environments, this strategy may increase mismatch risk as climate change shifts resource phenology. On land, Galápagos giant tortoises (*Chelonoidis* sp.) appear to track

## World Cup 2026 Host Metropolitan state areas



## Movebank studies



**Figure 3.** Identification of candidate movement studies for a scheduled anthropogenic event. Left panel: host metropolitan regions for the 2026 FIFA World Cup, delineated using metropolitan statistical area boundaries and equivalent administrative units. Right panel: temporal coverage of Movebank studies whose deployment centroids intersect host-region polygons and that extend towards 2026. Each horizontal segment represents the recorded deployment range for a species, with colour indicating the total number of tracked individuals. The vertical red band indicates the event window of interest.

long-term vegetation productivity and may exhibit reduced energetic efficiency when migration timing is mismatched with resource conditions [91].

### (c) Human–wildlife overlap, interactions and conflict

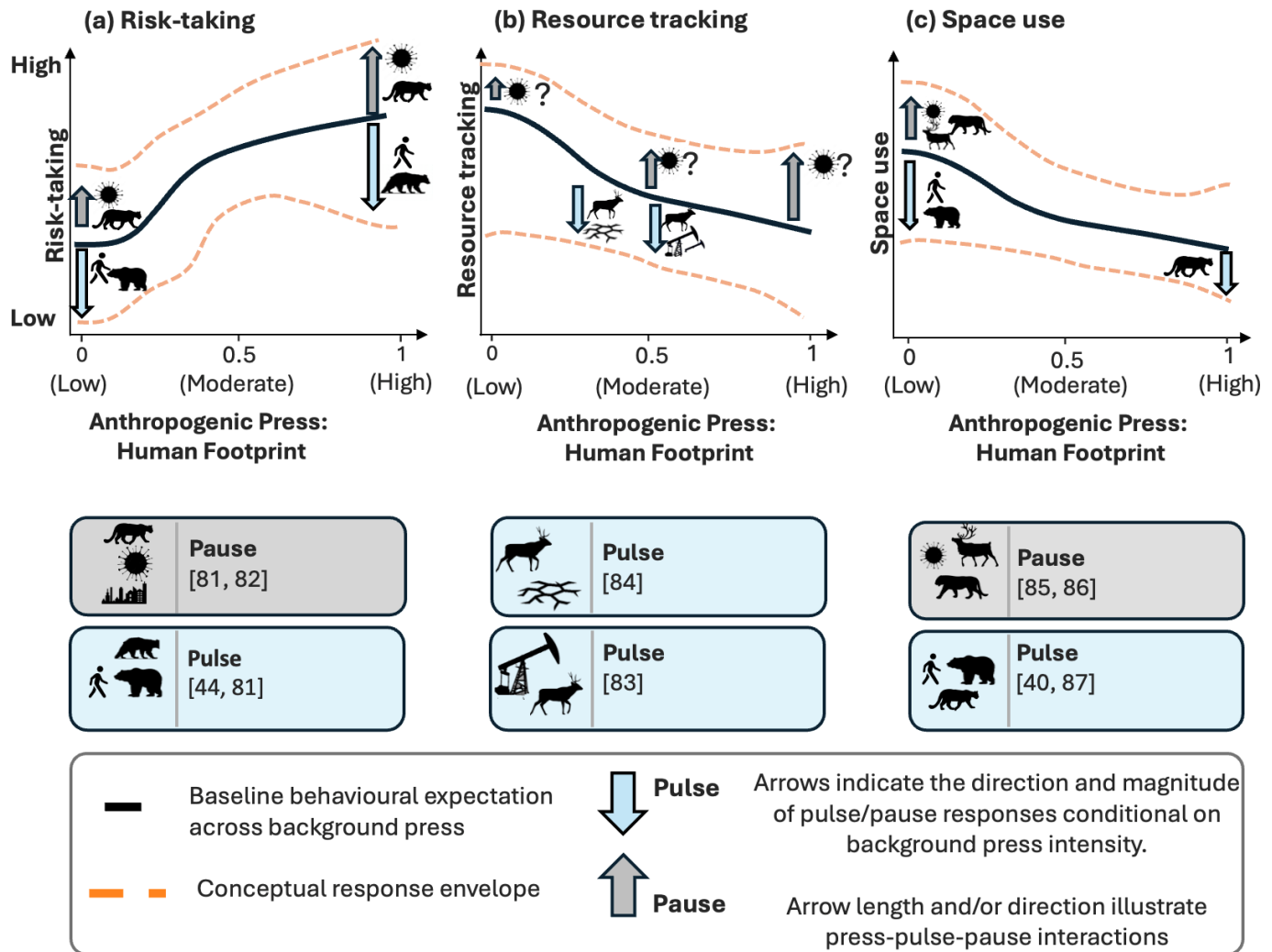
As evidence accumulates implicating human disturbances in amplifying global human–wildlife conflict, exploring how combinations of press–pulse–pause scenarios impact wildlife becomes increasingly more urgent. Specifically, leveraging current knowledge on wildlife risk-responses and space use both enables the formulation of testable predictions for human–wildlife interactions under varying combinations of anthropogenic and climatic disturbances, while also revealing pathways for effective human–wildlife coexistence.

Anthropogenic press disturbances—such as sustained urban expansion—have been identified as the primary drivers of increased human–wildlife overlap expected over the next 50 years [1]. As urban areas expand into previously natural habitats, wildlife is increasingly sharing space with humans, elevating the baseline risk for human–wildlife conflicts. Layering pulse and pause scenarios onto this press backdrop of expanding human presence may further increase the spatial overlap between wildlife and people. During periods of extended drought (pulse, Palmer Drought Severity Index), common bird species in the Central Valley of California, USA, increased their habitat association with agricultural and urban areas (press, Human Footprint Index), likely due to scarcity of water bodies [94], suggesting closer geographic proximity of wildlife with agricultural workers and urban residents near freshwater sources. An analysis of human–wildlife conflict reports in California further associated drought with increased conflict for carnivores and American black bears (*Ursus americanus*), potentially reflecting increased reliance on anthropogenic resources under resource limitation caused by this climatic pulse [95].

Across the United States, large mammals increase their utilization of forested areas during days of extreme heat (pulse, maximum daily temperature), reducing their presence in areas with higher human modification (press, Human Footprint Index) [96]. Consequently, humans recreating in forested areas (e.g. hiking, backpacking) could experience increased risk of coming into conflict with wildlife. Building on our earlier case study, during the COVID-19 lockdowns mountain lions (*Puma concolor*) increased their presence in and use of urban greenspaces in response to sharp declines in human mobility (pause, daily human mobility patterns) [82]. Although human movement declined during this period, human use of urban greenspaces which remained open to the public saw sharp increases [97], elevating the likelihood of human–wildlife encounters. Understanding wildlife responses to press–pulse–pause scenarios can help us predict and plan for when and where conflict hotspots may occur and identify key opportunities for enhancing coexistence and resilience.

### (d) Towards informed predictions of animal movement

Integrating behavioural mechanisms of movement ecology into the press–pulse–pause framework provides a valuable foundation for predicting wildlife resilience and vulnerability to compounded, overlapping anthropogenic pressures [6,88]. Our framework predicts that responses will depend on press intensity and behavioural plasticity. In systems where presses (e.g. gradual urban expansion) and pulses (e.g. sudden spikes in traffic) are linked in a predictable manner, wildlife may shift behaviour to cope with disturbances. However, in less predictable systems, organisms' ability to behaviourally cope may



**Figure 4.** Conceptual effects of anthropogenic pulses and pauses on animal behaviour across the gradient of anthropogenic press intensity, illustrated here using the human footprint index. Hypothesized responses are illustrated schematically for risk taking, resource tracking and space use. Grey arrows indicate pauses, while blue arrows indicate pulses. Arrows show the direction and relative magnitude of behavioural change caused by a pulse or pause at a given level of background anthropogenic press; variation in arrow length and/or direction across the x-axis illustrates hypothesized press-pulse-pause interactions. (a) Empirical examples include mountain lions (*Puma concolor*) which exhibited increased risk-taking in response to lower levels of human mobility during the anthropause in highly urbanized environments [82]. Similarly, other large mammals, such as bears, appeared to display larger changes in activity in response to the anthropause in highly urbanized areas [44] when compared with less developed landscapes [81]. (b) Mule deer (*Odocoileus hemionus*) exhibited a decline in resource tracking, specifically a reduction in 'green-wave surfing', or of following spring vegetation after the expansion of industrial gas fields (press). During an extended drought (pulse) mule deer also abandoned peak resource tracking and shifted migration timing away from vegetative phenology, illustrating how both sustained infrastructure development and acute water scarcity can reduce effective tracking of resource waves [83,84]. Displayed as grey arrows with question marks, we hypothesize that reduced human mobility during the COVID-19 induced anthropause may have increased resource tracking in wildlife, with the strongest increases in highly urbanized areas when compared with less disturbed landscapes. (c) Increases in human mobility in the form of outdoor recreation appeared to decrease the amount of space used by animals [30]. By contrast during COVID-19-driven reductions in winter recreation, woodland caribou (*Rangifer tarandus*) expanded their core use areas by 80–120% [85], and male Bengal tiger (*Panthera tigris*) home-range size tripled during Nepal's 2021 nationwide lockdown [86]. Citations provide examples of pulse and pause scenarios shaping wildlife responses as conditional on background press intensity [87].

be constrained, amplifying potential negative outcomes. This could facilitate the development of testable hypotheses, linking future press-pulse-pause scenarios to specific movement patterns (figure 4). In so doing, convergences between behavioural responses and specific disturbances may identify tipping points where the frequency or magnitude of the disturbance becomes intolerable, constraining adaptive plastic responses. When disturbances exceed these tipping points, they could then negatively affect demographic processes precipitating population declines.

### (e) Integrating other organismal biology disciplines

Integrating perspectives from other subdisciplines in organismal biology may be especially promising in assessing the extent of consequences incurred by wildlife when coping with human induced rapid environmental change. In behavioural ecology, movement activity, risk-taking and resource tracking represent a small subset of the traits known to vary in human-altered ecosystems [98–100]. Shifts in sociality, aggression, communication and parental care may disrupt or alter interactions among conspecifics, with cascading effects for population demography and persistence [101,102]. For instance, altered movement trajectories due to press-pulse-pause events may amplify exploratory behaviour, but reduce intraspecific interactions, erode

social group structure, reduce reproductive opportunities and exacerbate territorial conflicts, increasing instability in population dynamics [103]. An animal's cognition—which includes the processes of learning, attention, memory and decision making—also principally governs how individuals experience and respond to press–pulse–pause events. This may especially be relevant for pronounced yet predictable events, where individuals able to both successfully perceive environmental cues preceding a disturbance (e.g. increased traffic volume before a sporting event) and recall similar prior can adjust their responses accordingly, spotlighting memory and learning as essential for adequately responding to human disturbance [104,105]. Further, wildlife with sufficient cognitive innovation may be able to 'buffer' against novel, repeated or intensifying disturbances if the associated cues are reliable signals of future environmental conditions (i.e. the cognitive buffer hypothesis) [106].

Linking external disturbances (i.e. press–pulse–pause events) with observed behavioural patterns only partially articulates how wildlife experience such pressures. Examining the internal mechanisms (i.e. ecophysiology) that principally govern those behaviours provides a more holistic explanation for how wildlife cope with human disturbances. Coincidentally, the behavioural traits we previously identified (e.g. risk-taking, resource tracking, etc.) are intricately coordinated by the hypothalamic–pituitary–adrenal (HPA) axis, the primary neuroendocrine mechanism linking the central nervous system to endocrine function [107,108]. Stress physiology has justifiably garnered considerable attention in the literature, as released stress hormones (e.g. glucocorticoids) regulate the physiological and behavioural states behind the 'fight or flight' response when an animal encounters a disturbance [109,110]. We may predict that wildlife responses to acute pulse events induce adaptive coping responses that maintain homeostasis with little disruption to animal health or well-being. However, pulse events may present as chronic stressors that overly activate the HPA axis long-term, leading to deleterious effects from the overproduction of glucocorticoids (e.g. immunosuppression, reproductive dysfunction, cognitive decline, etc.) [108,111]. Resultant elevation in allostatic load (i.e. the accumulating 'wear and tear' due to compounding stressful events) may consequently increase disease susceptibility, leading to infected individuals with greater stochastic or aberrant movement patterns [112–115]. Increased spillover of zoonotic diseases may then have ripple effects for population- and community-wide health, shaping the risk-taking and resource tracking of entire trophic guilds [116]. Coincidentally, human-induced land use changes and projected increases in human–wildlife overlap [1] will probably drive heightened zoonotic spillover into human populations [117,118], emphasizing the urgency in diagnosing how press–pulse–pause events affect both behavioural and physiological traits.

## 4. Conclusion

Applying the press–pulse–pause framework within movement ecology enhances our ability to explore how different species respond to combinations of disturbances, but understanding why certain species cope better than others requires additional research. While we have connected different disturbance domains (e.g. extreme weather events and human modification) and linked these stressors to movement ecology and other aspects of animal behaviour, future work requires a comparative perspective of movement ecology to better understand what makes 'winners' and 'losers' in the Anthropocene [119]. Specifically, research comparing behavioural plasticity and movement responses across species facing various stressors, as well as investigating potential connections with other phenotypic or biological traits. Such investigations will contribute to a mechanistic understanding of why some organisms adapt or habituate more rapidly to presses and pulses, while others remain sensitive to even minor perturbations. Furthermore integrating movement ecology insights with conservation actions can enable more anticipatory and effective management strategies [62] such as dynamically regulating recreation and traffic during sensitive periods, or implementing temporary road-speed reductions when animals are most likely to cross. These insights have the potential to improve predictions of how human–wildlife conflicts might unfold under multiple simultaneous disturbances, aiding managers and policymakers in developing adaptive strategies that foster coexistence in a rapidly changing world.

**Ethics.** This work did not require ethical approval from a human subject or animal welfare committee.

**Data accessibility.** The codes used to recreate data driven figures of this perspective are available on GitHub (<https://github.com/diego-ellis-soto/PressPulsePause>). This article does not report newly generated primary empirical data.

**Declaration of AI use.** AI-assisted technologies were used to identify grammatical errors and improve spelling, grammar and flow. The authors reviewed all suggested edits.

**Authors' contributions.** D.E.-S.: conceptualization, investigation, project administration, supervision, visualization, writing—original draft, writing—review and editing; B.A.: conceptualization, writing—original draft, writing—review and editing; K.G.: conceptualization, writing—original draft, writing—review and editing; C.R.: conceptualization, writing—original draft, writing—review and editing; C.J.S.: conceptualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

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