
















# A vision for incorporating human mobility in the study of human–wildlife interactions

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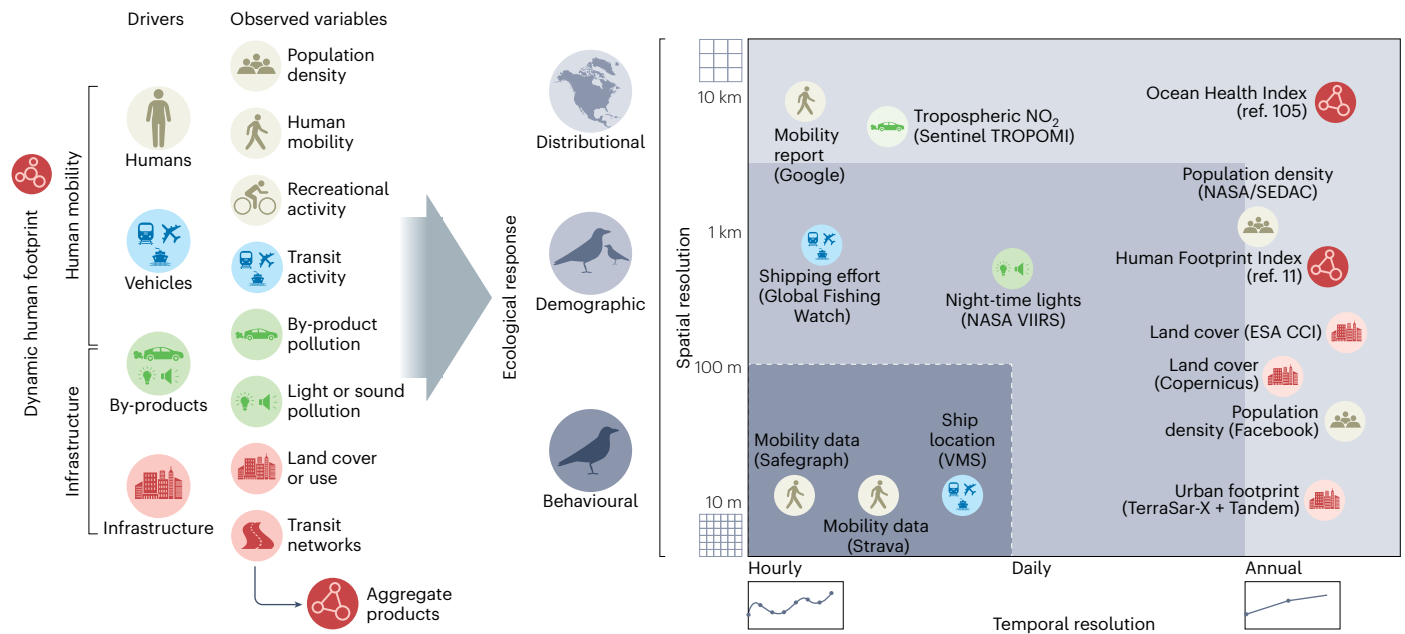
As human activities increasingly shape land- and seascapes, understanding human–wildlife interactions is imperative for preserving biodiversity. Habitats are impacted not only by static modifications, such as roads, buildings and other infrastructure, but also by the dynamic movement of people and their vehicles occurring over shorter time scales. Although there is increasing realization that both components of human activity substantially affect wildlife, capturing more dynamic processes in ecological studies has proved challenging. Here we propose a conceptual framework for developing a ‘dynamic human footprint’ that explicitly incorporates human mobility, providing a key link between anthropogenic stressors and ecological impacts across spatiotemporal scales. Specifically, the dynamic human footprint integrates a range of metrics to fully acknowledge the time-varying nature of human activities and to enable scale-appropriate assessments of their impacts on wildlife behaviour, demography and distributions. We review existing terrestrial and marine human-mobility data products and provide a roadmap for how these could be integrated and extended to enable more comprehensive analyses of human impacts on biodiversity in the Anthropocene.

Although humans have reshaped planet Earth for millennia, current impacts of anthropic activities are staggering<sup>1</sup>. More than half of the Earth’s surface—70% on land and 57% at sea—has been substantially altered by human activities<sup>2–5</sup> driving major changes in the behaviour, distribution and viability of wildlife populations<sup>6,7</sup>. Despite the negative consequences for biodiversity as a whole, a growing body of evidence suggests that behavioural plasticity and natural selection may enable adaptation to a changing world, even allowing some species to thrive in the Anthropocene<sup>8,9</sup>. The variable responses of wildlife to anthropogenic stressors indicate that the mechanisms governing human–wildlife interactions and coexistence are complex and context-dependent. As human pressures continue to increase,

there is an urgent need to understand how wildlife copes with current levels of human activity.

To study wildlife responses to human activities, ecologists have typically leveraged estimates of various aspects of anthropogenic influence, such as land development or human population density<sup>10–12</sup>. Integrated metrics of the human footprint have been widely useful in assessing the condition of ecosystems and protected areas globally and in predicting population trends and extinction risks by incorporating the many dimensions of human activities<sup>11,13–17</sup>. Though critical, the dynamic presence of humans and their vehicles (human mobility<sup>18</sup>) is often not captured by current approaches. Although landscape modification is a well-known driver of biodiversity loss, human mobility

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**Fig. 1 | Motivation for the development of a dynamic human footprint.** Left, the static and dynamic components of human activity. In contrast to static landscape modifications (for example, roads and buildings), human mobility encompasses the dynamic movement of humans and their vehicles. Drivers are quantified as a set of observed variables, ranging from relatively static assessments of infrastructure and population density to highly dynamic approximations of human mobility and aggregated products. These variables can then be used to examine potential ecological responses along a range of spatiotemporal scales. Right, the ecological scales that may be appropriate

for each observed variable as dictated by each variable’s associated spatiotemporal resolution. Approximate spatiotemporal resolution of example datasets and their corresponding ecological scale are indicated. The dashed rectangle highlights the current lack of publicly available datasets with high spatiotemporal resolution. For more details on a representative set of data sources, see Supplementary Table 1. CCI, Climate Change Initiative; SEDAC, Socioeconomic Data and Applications Center; TROPOMI, Tropospheric Monitoring Instrument; VMS, vessel monitoring system.

may also exert additional pressure on wildlife. Human mobility may represent a key link between anthropogenic stressors and ecological impacts by driving behavioural or demographic responses that scale up to consequences at the species level. However, information on human mobility has yet to be widely adopted in wildlife studies or integrated metrics of the human influence on nature.

As the COVID-19 pandemic unfolded, researchers started exploring opportunities to leverage human-mobility data products to examine how wildlife responded to lockdowns<sup>19</sup>. Until then, the ecological research community had been largely unaware of advances in measuring human mobility, which were driven by decades of work in other disciplines (for example, transportation, population geography, computer science, physics, public health and geographic information science) and the private sector<sup>20</sup>. The importance of monitoring and managing human movements to stem the spread of COVID-19 (for example, via social distancing and travel restrictions<sup>21</sup>) spurred some companies to make human-mobility data publicly available. This increased data accessibility created exciting opportunities for ecologists to investigate more comprehensively how wildlife is affected by humans—both during and after the COVID-19 anthropause. Human mobility has multiple components<sup>18</sup>. We consider human mobility to encompass the movements of humans and their vehicles (and any associated by-products in the environment), along the full spectrum of spatiotemporal resolutions. This is distinguished from human infrastructure, which encompasses roads, buildings and additional anthropogenic landscape modifications (and their associated by-products). Figure 1 provides a schematic overview of key concepts and terminology.

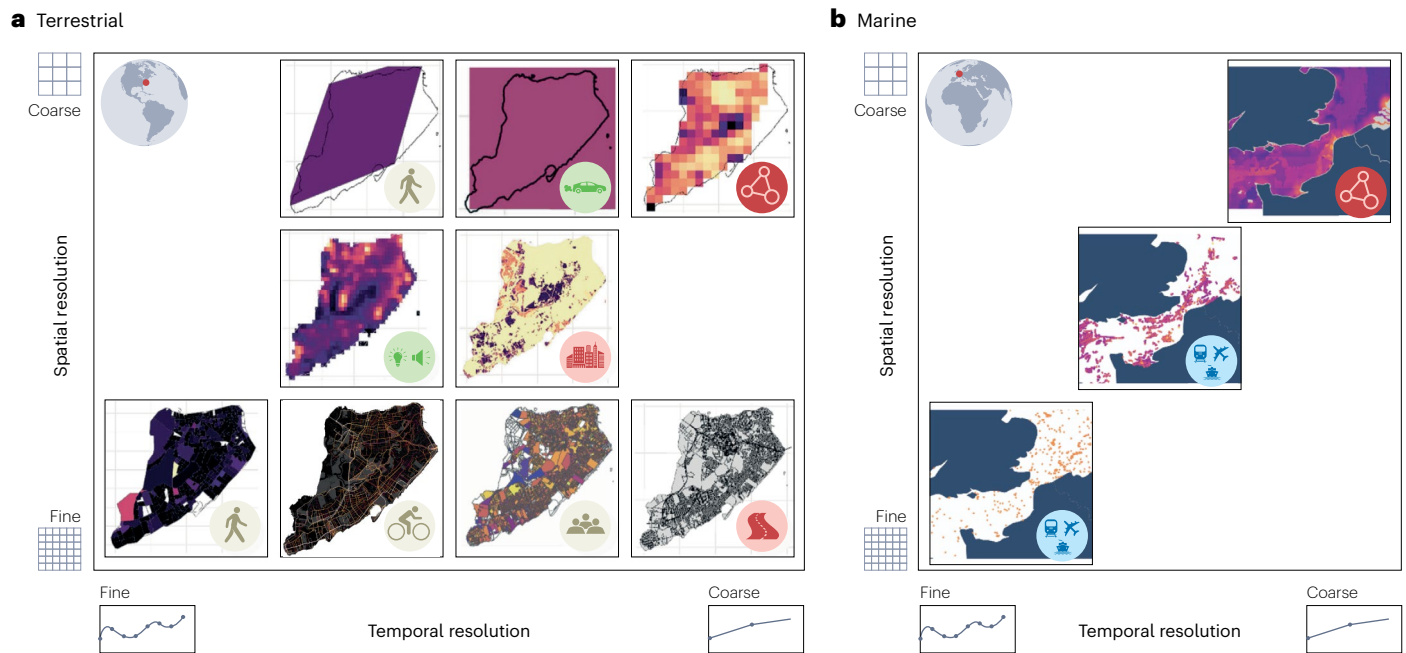
In this contribution, we argue that high-resolution human-mobility data should be combined with more conventional static measures (for example, population density and land-cover maps) to capture the multidimensional, dynamic nature of human activity and its complex

effects on wildlife. But doing so requires ecologists to understand the accessibility, underpinning and limitations of human-mobility data products. Although a handful of recent studies have begun integrating datasets reflecting static and dynamic components of human activity, they have been restricted to local and regional scales<sup>22,23</sup>, and their methods are not yet applicable to many other areas across the world, particularly in the Global South.

Here, we present a conceptual framework for integrating human mobility with other components of human activity into a multiscale dynamic human footprint. This vision builds on a rich literature quantifying human impacts on the planet<sup>24–26</sup>, extending it by explicitly incorporating the movements of humans and their vehicles. Our framework is ‘dynamic’ in two senses: first, in that it considers time-varying information on human mobility and, second, in terms of allowing flexible data aggregation across a suite of human activities (Fig. 1). We review existing terrestrial and marine human-mobility data products that are of relevance to the ecological research community but have not yet been widely adopted (Figs. 2 and 3, Supplementary Table 1). Using recent empirical examples, we then demonstrate how emerging metrics of human mobility enable refined investigations of anthropogenic impacts on wildlife behaviour, demography and distribution. We conclude with a set of recommendations for how the ecological community and other stakeholders can make progress towards integrating a variety of human mobility metrics to achieve a comprehensive analysis of human impacts on biodiversity in the Anthropocene (Fig. 4).

### Measuring human mobility

Here, we outline the main approaches for measuring the dynamic movement of humans and their vehicles. In 2021, mobile-phone subscriptions topped 8 billion worldwide, with over 6 billion of those subscriptions being registered to smartphones<sup>27</sup>. The proliferation of mobile devices means that we can capture human-mobility data across



**Fig. 2 | Measuring the dynamic human footprint. a, b,** Selected examples of datasets quantifying human activities in the terrestrial (a) and marine (b) realms. Spatiotemporal resolutions are presented qualitatively for comparison purposes only. Icons indicate the respective variable type, corresponding to those introduced in Fig. 1. a, Staten Island, New York (March–May 2020). Top row (left to right), mobility report at the community level (Google), tropospheric NO<sub>2</sub> (Sentinel-5 TROPOMI), Human Footprint Index<sup>10</sup>. Middle row (left to right),

night lights (NASA VIIRS), land-cover type (United States Geological Survey). Bottom row, (left to right), human mobility (SafeGraph), recreational activity (Strava Metro), population density (United States Census Bureau), road network (United States Census Bureau). b, English Channel (December 2019). Cumulative human pressures (top)<sup>3</sup>; fishing effort (Global Fishing Watch, middle); boat detection (NASA VIIRS, bottom).

broad spatial and temporal extents in most areas that are inhabited by people. Location data are now commonly collected using mobile phones relying on onboard GPS (Global Positioning System) receivers or by identifying the network node (Wi-Fi or cellular network tower) they are connected to<sup>20,28</sup>. Location-based mobile-phone services, such as real-time weather, social media and fitness applications, similarly collect high-resolution location data from their users<sup>29</sup>. The spatiotemporal resolution and continuity of these data vary greatly between technologies. Whereas GPS can yield accurate geographic coordinates, cellular tower networks provide data at spatial resolutions varying from very accurate in urban settings to relatively coarse in rural areas, depending on local network coverage. Furthermore, various types of human-mobility data vary in their temporal resolution. Data from cellular networks are often more temporally continuous than GPS data collected from smart-phone applications.

Although network and technology companies collect individually identifiable information, they do not typically make raw mobile-phone data (publicly) available because of geoprivacy concerns and compliance with national and international regulations (for example, General Data Protection Regulation of the European Union). Instead, human-location data are anonymized or aggregated to prevent the identification of individuals<sup>30</sup>. Mobile-network data are often aggregated into origin–destination flows, which provide information on how many users moved between two given geographic areas, such as the areas served by two mobile-phone towers<sup>31</sup>. Importantly, the quality of the estimates of human mobility derived from mobile-phone data varies based on the number of devices contributing data and, therefore, becomes less accurate in more sparsely populated regions. This is compounded by the fact that access to and usage of mobile devices vary across the globe<sup>21</sup> and that users of mobile phones, and of different applications, vary geographically and in terms of their sociodemographic characteristics<sup>32</sup>. Mobile-phone uptake rates vary greatly within and among countries, undercounting rural populations<sup>33</sup>.

Therefore, human-location data have inherent spatial, temporal and sociodemographic biases and may be especially limited in characterizing activities in rural areas<sup>34</sup>.

Mobile-phone-tracking logs remain one of the most challenging data sources to access. Some of these challenges stem from legitimate concerns over data privacy. However, there is an increasingly large industry of private intermediary providers that charge for access to aggregated mobility indicators (for example, Near Mobility, Outlogic and SafeGraph). In response to the COVID-19 pandemic, a number of private companies started making large amounts of anonymized human-mobility data publicly accessible. Human-location data derived from mobile phones have been widely used, for example, to plan and study the impact of government restrictions on human mobility during the pandemic<sup>35</sup>. Research applications of these data, however, are constrained by fairly rigid data formats (for example, aggregation or use of fixed reference baseline), which limit the potential for reprocessing<sup>36</sup>. For example, in the case of Google Mobility products, estimates of human use of ‘greenspaces’ combine national and local parks into a single index, which may obscure ecological responses. Perhaps most importantly, there is limited clarity on the long-term support of these public products, making research planning difficult and future replication attempts impossible. In some cases, researchers have started working directly with mobile-phone network operators to overcome these issues. The European Commission has asked national mobile-network providers to release their network data to its Joint Research Centre to build a COVID-19-mobility dashboard<sup>37</sup>. In general, there is considerable scope for strengthening collaboration between the collectors and holders of large human-mobility datasets and the wider research community.

An alternative to mobile-phone-based approaches are data relating to various types of transport. For example, vehicular transportation data have been used during the COVID-19 pandemic to explore changes in flow of vehicular traffic<sup>38</sup> and cycling behaviour, as local authorities provided additional space for recreation<sup>39</sup>. These types of data



**Fig. 3 | Timeline of the availability of different human-activity-data products.** Lifetime of current data products, demonstrating the recent availability of many human mobility datasets from 2000 to 2022 (some products have been available for longer). Datasets are grouped and coloured by categories of drivers,

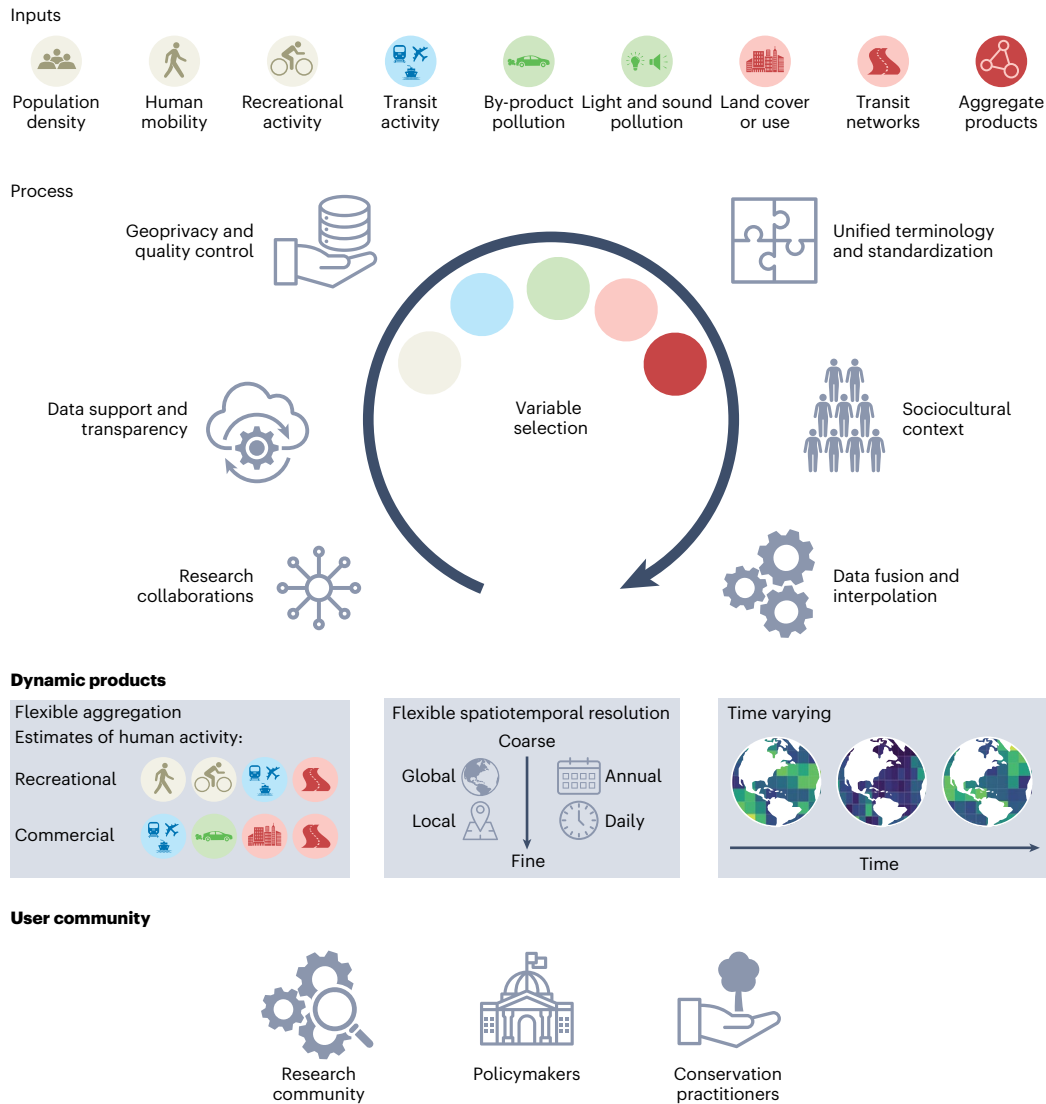
as introduced in Fig. 1. For details on the spatiotemporal resolution and extent of terrestrial, aerial and marine datasets, see Supplementary Table 1. MODIS, Moderate Resolution Imaging Spectroradiometer.

are commonly accessible through open data portals housed by local municipalities (for example, <https://tfl.gov.uk/info-for/open-data-users/our-open-data?intcmp=3671> and <https://www1.nyc.gov/site/tlc/about/tlc-trip-record-data.page>) or national authorities, presenting a major advantage over mobile-phone data in terms of accessibility. The main disadvantage of these datasets is that they are typically collected idiosyncratically at specific locations, most often in urban environments, making them unsuitable for studies in more remote areas or at larger geographic scales (for example, ref. 40). Other types of human mobility, such as those related to agriculture, forestry and hunting, are either documented through land-cover proxies or left uncharacterized.

In contrast to the more regional nature of data collection in terrestrial realms, marine traffic is monitored globally by the automatic identification system (AIS)—an anti-collision network that combines transceivers on ships and both in situ and satellite radar receivers to monitor ships' locations. AIS data are available through private companies and governmental institutions. For example, European marine data can be requested through the SafeSeaNet initiative. These data have been used to study the impacts of vessel traffic, and resultant noise pollution, on wildlife<sup>41</sup>, as patterns of global fishing effort<sup>42,43</sup>, and the

global reduction of marine traffic during the COVID-19 anthropause<sup>44</sup>. Marine traffic has also been monitored with night-light data from Visible Infrared Imaging Radiometer Suite (VIIRS) and VIIRS Boat Detection across scales, from individual vessel detections per night to annual summary grids of detection tallies and average radiances<sup>45</sup>. The global scale of marine data that are available at relatively fine spatiotemporal resolution, coupled with their good accessibility, provide ecologists with opportunities for broad-scale analyses that presently are out of reach for terrestrial studies. That said, activities such as recreational fishing cannot currently be assessed at local scales, limiting our understanding of reported increases in recreational marine human activities during the COVID-19 pandemic<sup>46</sup>.

Air traffic can be tracked through data on the total number of flights by FlightRadar24. Additionally, data on passenger flows are available for Europe through the European Union Open Data Portal, for the USA through the International Civil Aviation Organization COVID-19 Air Traffic Dashboard, and for 35,000 city-pairs around the world through the Civil Aviation Data Solutions portal. Air traffic was severely impacted during the COVID-19 pandemic, with temporary, but significant, reductions in commercial flights<sup>47,48</sup>.



**Fig. 4 | Constructing the dynamic human footprint.** A framework for a dynamic human footprint, leveraging a suite of input variables quantifying human mobility and infrastructure. Fundamental to achieving this vision is an integration process that begins by allowing users to select the human-activity variables relevant to their application target. Dynamic measures of human mobility are primarily held by private companies; their use depends on continued support to make them available to the research community (post-pandemic), transparency about data collection and processing, and robust protocols to ensure geoprivacy and quality control. Cross-disciplinary collaboration will be necessary for developing the methodologies necessary

for integrating disparate datasets across spatiotemporal resolutions. This in turn will require a unified terminology, to discuss the various components of human activity, and will be greatly assisted by adopting a standardized schema of data-processing levels, to distinguish raw data from modelled or aggregated data products. In many cases, data fusion or interpolation approaches will be needed for areas where human-mobility data are unavailable, which consider the underlying sociocultural context. This process will generate a suite of products that are inherently dynamic, both in terms of their flexible aggregation and their ability to generate time-varying estimates of human activity.

Complementary satellite-sensed data on artificial night lights and other by-products, such as nitrogen dioxide from fossil fuel combustion, have been used to measure aspects of human activity<sup>49,50</sup>. For example, artificial night lights have been used for mapping both vehicles and infrastructure, from maritime traffic to whole cities<sup>50,51</sup>. However, these products only capture activities that occur at night and produce high-powered lighting, which must be taken into consideration when charting spatiotemporal patterns in human mobility. These data are available directly from the NASA (National Aeronautics and Space Administration) [Earth Data centre](#). Daily satellite data on concentrations of various atmospheric gasses have global coverage<sup>52</sup> and are also available from the NASA [Earth Data centre](#) and from the Sentinel-5 Precursor satellite of the European Space Agency (ESA). For example, the [TROPOMI](#) sensor on-board of the Sentinel-5 Precursor satellite provides measurements of atmospheric gases,

including the most common anthropogenic pollutants, such as NO<sub>x</sub>, SO<sub>2</sub> and ozone. Satellite-recorded night-time images indicated dimming of light in China<sup>50</sup>, and NO<sub>2</sub> data documented decreases in pollution levels across European cities because of COVID-19-related changes in human activity<sup>45,53</sup>. One obvious limitation of by-product analyses is that it is challenging to estimate the relative contributions of dynamic and static components of human activity, which—as we have argued above—is key for advancing our understanding of ecological impacts.

### Inputs to a dynamic human footprint

In isolation, each of the data types discussed above provide a valuable window into how humans use different spaces over time, but in combination, they reveal the diversity of our impacts on the environment. Current approaches to mapping the global influence of humans, particularly the Human Footprint Index<sup>11</sup> and the Human Modification

map<sup>25</sup>, aggregate multiple aspects of the built environment—including infrastructure, land use and transportation networks—along with static estimates of human population density and distribution. These indices have been used extensively, and very productively, for assessing wilderness loss, protected area effectiveness and wildlife responses to human encroachment (for example, refs. 12,15,54–56). Recent advances in machine learning mean that human footprint maps may be generated more rapidly, allowing for greater temporal resolution<sup>57</sup>. Considering the increasing availability of high-quality human-mobility datasets, we see an opportunity for extending the concept: developing a vision for a framework for quantifying humans' dynamic footprint on Earth would allow for the investigation of ecological processes (for example, wildlife movement and related behaviours) that occur over much shorter time scales (for example, integrating data over a migratory journey that lasts a few weeks, rather than across years or longer periods, as current measures do).

Our proposed dynamic human footprint incorporates the multiple ways in which humans affect environments, by aggregating both static and dynamic metrics spanning the full range of spatiotemporal scales. Importantly, rather than computing a single index, we envision a modular set of products that can be tailored to the specific research question and ecological responses under investigation (Fig. 1).

The underlying datasets supporting these footprint estimates depend on which drivers and spatiotemporal resolutions are required to link different types of human activity to ecological processes. Questions related to distributional changes for wildlife may require a global-scale, coarse-grained, human-footprint estimate<sup>42</sup>, whereas questions related to behavioural responses would necessitate a fine-grained approach, potentially limited to select locales (for example, ref. 22) (Fig. 1). For example, understanding behavioural responses of animals to COVID-19 lockdowns would benefit from quantifying changes in human mobility at high spatiotemporal resolutions (for example, metres and hours)<sup>19,58</sup>. If conducted globally, the footprint estimates for such a study would require all underlying datasets to have global extent or rely on modelling approaches for appropriate interpolation. By contrast, a study with a more limited geographic scope would be able to leverage datasets that are only available locally, such as municipal traffic-flow estimates. In general, our review in the previous section reveals a striking lack of widely available human-mobility data products that could be used to address ecological responses at finer spatiotemporal scales (Fig. 1).

The development of such products would ideally be based on the data-processing levels employed by the NASA [Earth Observing System Data and Information System](#) and the ESA's Earth observation [data access portal](#). Under this system, data products are classified along a scale from raw, unprocessed data (level 0) to corrected data (level 1), derived variables (levels 2–3), and, ultimately, modelled outputs (level 4). In the context of a dynamic human footprint, each dataset would be rated corresponding to its processing level. For example, unstandardized mobile-device counts may be considered a level 0 product, whereas population-density estimates may be considered a level 3 product. Combined datasets, such as daily aggregate products of human mobility, would be given a level 4 distinction, to indicate their synthetic nature. A critical challenge in this process will be appropriately measuring the uncertainty propagated from underlying data sources to derived products.

As noted above, aggregating across data types will be at the core of the dynamic human footprint (Fig. 4). When integrating datasets with similar spatiotemporal resolutions and extents, we propose following previous approaches that rely on standardizing values within and among datasets (for examples, refer to refs. 11,25). This step alone is not necessarily straightforward, as it requires handling mismatches in resolutions and a nuanced understanding of the rescaling methods appropriate for different data types. However, we also envision scenarios in which the variables of interest are not readily available across

the full extent required, necessitating more sophisticated methodologies for interpolation. This would apply, for example, to high-resolution transit or human-mobility data that are not currently available at global, or even regional, scales (see above). It may be possible to compute finer-scale human-mobility estimates by modelling statistical relationships between coarse mobility data and satellite-sensed auxiliary data, which serve as a proxy for finer-scale movement<sup>59,60</sup>. But this would probably involve the use of complex data-fusion methods and modelling techniques, including Bayesian approaches, for leveraging the respective best qualities of different human-mobility datasets<sup>59,61</sup>.

For example, data on the fine-scale spatial structure of outdoor recreation activity as delivered by fitness apps such as Strava could be combined with mobile-phone data (for example, Google Mobility reports) to generalize the temporal dynamics of such activities<sup>22</sup>. In general, such approaches need to be employed cautiously, as human mobility is linked, as we had noted above, to a complex set of cultural, sociodemographic and environmental factors that vary geographically and must be accounted for<sup>62,63</sup>. Aggregating across data types will require explicit and careful consideration of the underlying sources of uncertainty and potentially compounding biases. For example, estimating population density by downscaling census data using mobile-phone call records compared with using remote-sensing data has been shown to have opposing trade-offs in accuracy and precision<sup>33</sup>. Remote-sensing-based approaches underestimate population density in dense areas and overestimate it in less populated areas, whereas the opposite has been found for mobile-phone data<sup>33</sup>. However, combining methods delivered overall improved accuracy<sup>33</sup>. Therefore, users should carefully assess the systematic uncertainty and biases of different data types and, as much as possible, leverage the complementarity of data sources and types through integration.

In the following sections, we use recent empirical examples to showcase how a dynamic human footprint could be employed to advance our understanding of human–wildlife interactions and their effects on behaviour, demography and distributions. The datasets used in these case studies remain limited in their applicability and availability: at fine scales, they are often collected idiosyncratically (for example, AIS<sup>64</sup>), whereas at coarse scales, they remain relatively rough proxies of human activity. Therefore, we see these examples as demonstrating the need for a dynamic human footprint that enables research on human–wildlife interactions at appropriate—and as yet largely unachieved—spatiotemporal scales.

## Behavioural responses

The 'ecology of fear' hypothesis suggests that the risk of predation alters prey behaviour and physiology in the absence of direct mortality<sup>65</sup>. A 'landscape of fear' is a species' perception of the spatiotemporal patterns of that risk as a result of predator activity<sup>66</sup>. Because many animals are thought to perceive humans as super predators<sup>67</sup>, the landscape of fear hypothesis predicts that animals will avoid human-occupied areas in a similar fashion as they might avoid areas frequented by predators<sup>68,69</sup>. Such human avoidance can manifest in both spatial and temporal shifts in activity. For example, many animals become more nocturnal in the presence of humans<sup>70</sup>, and some prey species select areas of high human mobility, to 'shield' themselves from predators (that is, the human shield hypothesis)<sup>71,72</sup>. Furthermore, the response may differ depending on the type of activity, such as the use of motorized versus non-motorized recreational vehicles<sup>73</sup>. As such, to study behavioural responses of wildlife, human-mobility datasets should have high temporal resolution to capture the dynamic nature of humans' movements across habitats (Fig. 1; for example, sub-daily human mobility or traffic data that can be collected at <1-km<sup>2</sup> resolution).

Implicitly or explicitly incorporating dynamic human-activity data can often help to understand animals' behavioural responses. For example, by integrating land-cover and anthropogenic noise data, the

song frequency of white-crowned sparrows (*Zonotrichia leucophrys*) was found to increase in response to early COVID-19 lockdown in the San Francisco Bay area<sup>74</sup>. By contrast, great white sharks (*Carcharodon carcharias*) showed no change in space use at a seal colony in South Australia when cage-diving tourism operations paused for 51 days during lockdown<sup>75</sup>. By integrating dynamic human-mobility data, such as driving and walking<sup>76</sup>, researchers were able to demonstrate that mountain lions (*Puma concolor*) in California ventured deeper into urban areas during the COVID-19 pandemic. These studies demonstrate the impacts of reduced human mobility with little or no corresponding change in infrastructure, indicating that dynamic and static metrics are not redundant measures of human activity.

### Demographic responses

Human activities can influence wildlife populations by affecting critical life history stages. Vital rates (for example, survival and fecundity) can be altered over a wide range of temporal scales (that is, days to years) and, therefore, require human-activity data of moderate spatiotemporal resolution (Fig. 1). Human disturbance can occur even in areas with relatively intact habitat if they attract visitors pursuing recreational activities. Outdoor recreation differs substantially throughout the week (for example, weekends versus weekdays) and is often spatially heterogeneous, with some areas being used more frequently than others<sup>77</sup>. These differences in human mobility may have substantial impacts on demographic responses. For example, recreational use of beaches impacted piping plover (*Charadrius melodus*) demographics by lowering chick survival during weekends and in areas of intense use<sup>78</sup>. Roads, vehicle traffic and collisions also cause wildlife mortality<sup>79</sup>. Traffic reductions during early COVID-19 lockdowns in central Europe led to sharp decreases in road mortality in large mammals, such as roe deer, but increased collisions with badgers indicating heterogeneous effects on demographic responses across species<sup>80</sup>. However, human impacts on demography must not necessarily be negative. For example, a seabird colony in the Baltic was typically shielded by tourism from gulls and crows<sup>81</sup>. When tourism declined during COVID-19 lockdowns, visitation rates by white-tailed eagles (*Haliaeetus albicilla*) drastically increased, causing—through disturbance, rather than predation—a 26% decrease in the productivity of common murre (*Uria aalge*). These nuanced responses of species to human recreation highlight the importance of integrating spatially explicit and temporally dynamic information on human mobility into ecological studies.

Recent advances in detecting sensory pollutants are offering insights into how humans affect demographic processes of wildlife across larger scales<sup>82,83</sup>. For example, datasets on anthropogenic noise and artificial light sources across the USA were combined with citizen science bird observations to show that demographic responses to these pollutants, and adjustments in phenology<sup>84</sup>, depended on species traits and habitats<sup>85</sup>. These results emphasize that the impacts of human activities are not uniform across species and that analyses must consider context dependence<sup>72,86</sup>. This is key to informing the design of effective conservation interventions<sup>83</sup>, such as reducing night-light emission during peak migration periods or limiting recreational activities during critical times of the breeding cycle<sup>87</sup>.

### Distributional responses

Metrics that characterize the amount of static human infrastructure in an area are the predominant source of information used to study anthropogenic impacts on species distributions<sup>88,89</sup>. Interactions among static and dynamic components of human activity may determine the magnitude and direction of anthropogenic impacts on species abundances and distributions. For example, static (human population density and human footprint) and dynamic (human noise and artificial night light) data were coupled with information on bird observations around feeder locations to reveal impacts on the abundance of several bird and mammal species at continental scale<sup>23</sup>. Similarly, by combining

the static Human Footprint Index with direct records of the presence of humans captured by camera traps, thresholds at which species with different traits are able to persist in human-dominated landscapes were identified<sup>90</sup>.

Although some changes in species distributions can occur abruptly over relatively short time periods, the ranges of individuals, populations and species are typically measured at coarser spatiotemporal resolutions. The integration of static and dynamic variables into a dynamic human footprint will allow us to more accurately predict how the distribution of species may change in response to human by-products (such as anthropogenic noise and artificial night lights) and human encroachment<sup>23,72,91</sup>. Modelling encroachment in a more detailed way may allow us to identify thresholds of anthropogenic development<sup>92</sup> or human-mobility levels, beyond which animal populations cannot persist. For example, light pollution may lead to nocturnal species abandoning or avoiding areas that would otherwise be suitable<sup>72</sup>. This may aid our understanding of the 'silent forest' concept, which posits that species may be absent in an area because of human activities, despite having suitable environmental conditions.

The activities of humans are a major driver of species extinction and exert strong selective pressure on the evolution of species<sup>93</sup>. The ability to consistently map human modification showed that mammalian genetic diversity and effective population sizes are lower in urbanized areas when compared with natural areas, but less so for birds<sup>94</sup>. Furthermore, sociodemographic disparities, such as economic inequality and racial segregation, appear to reduce overall genetic diversity in terrestrial mammals, reptiles and amphibians<sup>95</sup>. A dynamic measure of human activities would allow quantifying the degree to which human activities may affect behavioural plasticity and evolution and more importantly allow a framework to document behavioural changes of wildlife across a gradient of human activities in both space and time. Such a dynamic measure would allow a much more detailed exploration than the urban–rural gradient, as some rural areas experience very high and consistent seasonal influx of humans.

### A roadmap for data and collaboration needs

The successful development of a dynamic human footprint critically depends on closer collaboration among research communities, better connecting insights and approaches from the fields of ecology, conservation biology, environmental science, geographic information science, remote sensing, human geography, transportation science and social science. To bring this vision to life will require engaging with a diverse array of government agencies, local authorities, policy-makers and private industries. In the following sections, we provide a forward-looking vision for facilitating these interactions and for collaboratively tackling specific challenges.

#### Unify terminology

Productive collaboration will require a consistent, unified terminology for discussing concepts, methods, development goals and implementation strategies. We, therefore, urge the wider research community to adopt a standardized set of definitions. From an ecological perspective, terminology in this realm is complicated by the wide range of use cases and associated scales of analysis. Our proposed dynamic human footprint uses recently established definitions that clearly distinguish between static and dynamic components of human activity<sup>18</sup>.

#### Establish data standards

We encourage all parties that create and use human-mobility data to adopt a standardized representation and classification system for describing datasets, building upon approaches employed by the NASA Earth Observing System Data and Information System. Doing so would create transparency across scientific communities and correctly distinguish between raw data and modelled or aggregated products. Adopting an existing schema already in use would promote collaboration with

the remote-sensing community and other fields (such as the animal tracking community)<sup>96</sup>. Aligning the methods and data standardization used for human and animal tracking will be essential for future efforts to merge these data streams<sup>96</sup>. We also urge greater collaboration across disciplines to ensure that end users understand the limitations of data sources and select them based on appropriateness for their application as opposed to ease of access.

### Commit to data sharing and long-term support

Commitments from private companies to continue making human-mobility data products freely available will be important for future studies on human–wildlife interactions in the Anthropocene. To date, most large data providers explicitly state that **mobility reports** are publicly available for a limited time to help to stem the spread of COVID-19, suggesting that access may become restricted post-pandemic. Committing to data sharing and long-term support does not require releasing raw data and algorithms, which would raise privacy, ethical and commercial concerns. Anonymized, aggregated human-mobility data products can afford invaluable insights into human–wildlife interactions, and should be made available to the wider research community.

### Increase transparency and flexibility in data aggregation

Considering that data preprocessing can have notable effects on research outcomes, we urge private companies to provide greater clarity about the methods used to generate currently available human-mobility data products. Furthermore, we recommend that a higher degree of flexibility be incorporated into aggregate products. Allowing researchers to select the temporal baseline and categorical binning of aggregate mobility products would enable comparisons across different data sources and support a much broader range of research applications. This is of particular relevance for studies of animal species that routinely cross national borders, such as migratory species<sup>97,98</sup>.

### Address social, demographic, economic and cultural factors

Socio-economic dimensions are increasingly being integrated into ecology and conservation research to demonstrate the myriad impacts of structural inequality<sup>99–101</sup>. Clearly, patterns in human mobility are driven by a complex set of social, economic and cultural factors. For example, the worldwide total activity of fishing vessels records its lowest levels during the Chinese New Year, Christmas and New Year<sup>44</sup>. In the Middle East, the religious celebration of Ramadan, which typically greatly influences the mobility and behaviour of humans across large areas, was significantly disrupted during the COVID-19 pandemic<sup>102</sup>. We, therefore, urge close collaboration with human geographers and social scientists during the development of the dynamic human footprint.

### Develop systems to monitor change

It will be important for policymakers and funding agencies to support research and private–public partnerships that enable a dynamic understanding of humans' footprint on Earth. As the COVID-19 pandemic acutely illustrated, society was poorly prepared overall for changes in human behaviour on large scales and is still grappling to understand the implications across sectors. For example, how the COVID-19 pandemic has impacted biodiversity across the world, and thus affected progress towards the United Nations Sustainable Development Goals 14 and 15 (life on water and life on Earth), remains mostly unknown (but see ref. 48). We, therefore, need to develop a higher degree of preparedness for mapping changes in human mobility and measuring their environmental impacts<sup>48</sup>.

### Construct the dynamic human footprint

Being inherently dynamic in nature, the dynamic human footprint will require open-ended development. Therefore, this endeavour should embed flexibility with regard to choosing data sources and modelling

approaches, accommodating any future advances. In many regions of the world, high-resolution data on human mobility will be nearly impossible to collect. This is because of a variety of factors including differences in the geographical distributions of human populations, socio-economic inequalities, technological infrastructure, seasonality, privacy concerns and geopolitics<sup>103</sup>. Therefore, globally, or even regionally, consistent maps of the dynamic human footprint will require modelling and data-fusion approaches, which are likely to pose substantial development challenges.

### Conclusions

As the planet becomes increasingly crowded, we need to understand the complex interactions between humans and wildlife if we are to safeguard biodiversity for generations to come. Achieving this demands a rigorous accounting of the multidimensional aspects of human activity. We see an immense, time-sensitive opportunity for the ecological community to engage with other disciplines, to integrate data across spatiotemporal scales and operationalize a dynamic human footprint. Human-mobility data providers can make invaluable contributions to these efforts by improving data accessibility, data standardization and transparency. The insights gained by incorporating a dynamic human footprint into ecological studies could provide decision-makers with critical novel information for designing highly effective, targeted conservation interventions. Coordination and collaboration are imperative for understanding and managing human–wildlife interactions in the Anthropocene<sup>104</sup>. We must tackle this challenge with utmost urgency to protect the animals that are forced to share space with us.

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### Author contributions

D.E.-S. and R.Y.O. co-conceived and conceptualized the article with significant contributions from C.R. and W.J. and feedback from all co-authors (V.B.-B., U.D., B.J., J.A.L., F.C., F.O., N.Q., M.H., R.K., M.-C.L., T.M., R.P., D.W.S., M.A.T. and Y.R.-C.). D.E.-S. and R.Y.O. led the writing of the article with significant contributions from C.R., input from V.B.-B., J.A.L. and U.D., and feedback from all co-authors. D.E.-S. and R.Y.O. led the development of the figures with input from C.R., W.J., V.B.-B., N.Q., B.J. and R.P. and feedback from all co-authors (V.B.-B., U.D., B.J., J.A.L., F.C., F.O., N.Q., M.H., R.K., M.-C.L., T.M., R.P., D.W.S., M.A.T. and Y.R.-C.). Preparation of the article was coordinated by D.E.-S., R.Y.O., C.R. and W.J. All co-authors approved the submission of the article.

### Competing interests

The authors declare no competing interests.

### Additional information

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