Mammal species composition reveals new insights into Earth's remaining wilderness

R Travis Belote[1*], Søren Faurby[2,3], Angela Brennan[4], Neil H Carter[5], Matthew S Dietz[6], Beth Hahn[7], William J McShea[8], and Josh Gage[9]

Maps of the human footprint allow ecologists to identify the wildest lands on the planet, track their decline, and prioritize wildland conservation efforts. Other research efforts have mapped biological intactness and identified conservation priorities to protect biodiversity. However, little research has involved the use of historical references to evaluate intactness of species composition globally. We used a dataset estimating historical and current distributions of mammals to address whether the wildest places on Earth support the most intact mammal communities. Contrary to our expectations, we found that the global human footprint was not strongly correlated with mammal community intactness and uncovered surprising situations where both the human footprint and mammal species intactness were high, and other examples where both were low. Our results could be used to enhance maps and estimates of global wilderness areas by identifying wild and intact regions, while also prioritizing conservation of intact but human-modified landscapes.

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Humans impact ecosystems nearly everywhere on Earth, resulting in loss of wildlands (Venter *et al.* 2016; Watson *et al.* 2016) and extinction of species (Dirzo *et al.* 2014). Species extirpations caused by human development have been described as eroding the biotic intactness (Scholes and Biggs 2005; Newbold *et al.* 2015, 2016) and ecological integrity (Theobald 2013; Kennedy *et al.* 2019) of ecosystems. Biotic intactness and integrity are generally determined by the "wholeness" of ecological components (Aplet 1999). For example, ecosystems that maintain the full complement of natural processes and species that historically characterized a particular area are considered to be more intact and to have higher ecological integrity than those that do not (Scholes and Biggs 2005; Morrison *et al.* 2007).

Historical references are often used to create targets when restoring degraded ecosystems (Keane *et al.* 2009; Corlett 2016). However, empirical baselines, or starting points, for measuring departures from historical species composition are rare and often fail to capture all species within a taxonomic group (Laliberte and Ripple 2004; Morrison *et al.* 2007); as such, efforts to produce global maps of biological integrity have largely relied on contemporary references to assess relative intactness (Newbold *et al.* 2016). Mapping areas in which the natural community includes the full complement of species that existed historically is challenging (Newbold *et al.* 2016; Pimm *et al.* 2018), but such efforts could provide important insights into global conservation priorities (Pimm *et al.* 2018).

Recent assessments of global conservation priorities have mainly focused on mapping the "last of the wild" to call attention to the remaining ecosystems without substantial human infrastructure or land-cover conversion (Watson *et al.* 2016, 2018). However, to date we know little about how the human footprint relates to ecological intactness as measured by shifts in species composition from historical baselines. Ecological integrity (Theobald 2013) and biological intactness (Scholes and Biggs 2005; Newbold *et al.* 2015) are typically expected to be highest in the wildest, least human-modified lands, given that the human footprint is associated with species' extinction risk (Di Marco *et al.* 2018, 2019). However, the extent to which human development affects species extirpations can be species- and context-dependent (Luck 2010; Fahrig 2017; Allan *et al.* 2019). Some species differ in their sensitivity to human activities, with responses depending on environmental conditions or plant productivity (Luck 2007). Species living in arid lands, for instance, may be particularly sensitive to human impacts (Chillo and Ojeda 2012), and the life history and diet of certain omnivorous species enable coexistence with human settlements (Fedriani *et al.* 2001).

Human cultural relationships with mammals can also influence the composition of mammal communities (Carter *et al.* 2014). In recent times, for example, population strongholds of some flagship mammal species (eg African savanna elephant [*Loxodonta africana*]) have been largely confined to protected areas as a result of conservation efforts and the human development occurring outside of these areas (van Aarde and Jackson 2007). Anthropogenic disturbance and landscape alteration have markedly affected the movement

[1]*The Wilderness Society, Bozeman, MT *(tbelote@tws.org);* [2]*Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden;* [3]*Gothenburg Global Biodiversity Centre, Gothenburg, Sweden;* [4]*World Wildlife Fund, Washington, DC;* [5]*School for Environment and Sustainability, University of Michigan, Ann Arbor, MI;* [6]*The Wilderness Society, Oakland, CA;* [7]*Aldo Leopold Wilderness Research Institute, Missoula, MT;* [8]*Smithsonian Conservation Biology Institute, Front Royal, VA;* [9]*Gage Cartographics, Bozeman, MT*

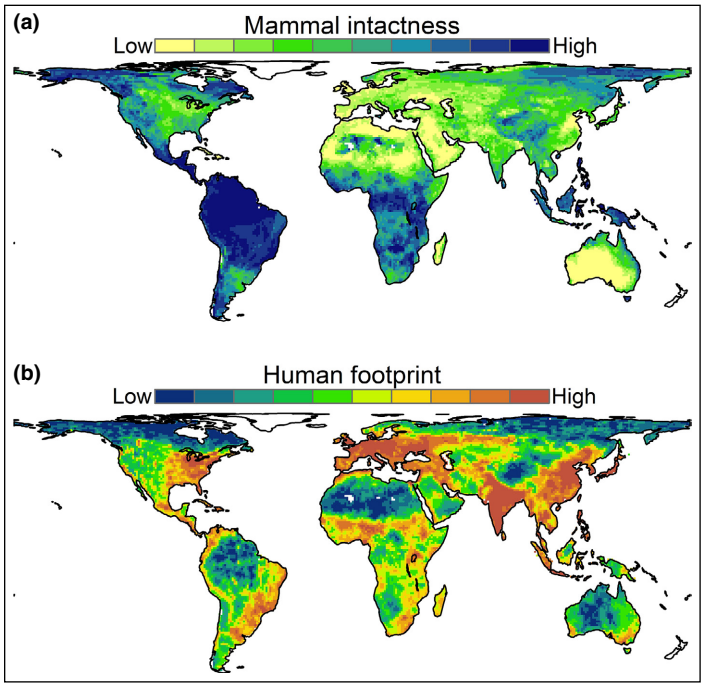

Figure 1. (a) Map of mammal intactness (ratio of current to historical species richness), based on data from Phylacine 1.2 (Faurby *et al.* 2018), which contains data modified from Faurby and Svenning (2015). (b) Map of the global human footprint, based on Venter *et al.* (2016) after removing pixels where historical richness <15 species. The resolution of both maps is 96.5 km, and both are projected using WGS 1984 Cylindrical Equal Area.

patterns of large migratory species (Harris *et al.* 2009). Because they were perceived to pose intolerable risks to human livelihoods and safety, large carnivores have been eradicated from many landscapes (Ripple *et al.* 2014). Hunting and poaching for sport or consumptive use, and conflicts with agricultural practices, have also caused substantial depletion, and in some cases extirpation, of large herbivore populations.

We investigated whether the magnitude of the human footprint is associated with intactness of species' assemblages and whether this relationship is affected by the abiotic environment or estimated plant productivity. We used recently developed global maps of estimated historical and current distributions of mammals (Faurby and Svenning 2015) to calculate an index of mammal community intactness. We then examined the relationship between the human footprint and mammal community intactness. We predicted that the least human-modified lands would be the most intact with respect to maintaining historical mammal species composition. Finally, we investigated whether environmental factors (climate, topography, soils, and primary productivity) interact with the human footprint and mammal community intactness.

Methods

We calculated mammal community intactness using maps of historical and current geographic distributions of mammals based on data from the Phylacine 1.2 database (Faurby *et al.* 2018), which contains data from Faurby and Svenning (2015) and the International Union for Conservation of Nature 2016-3. The data we used for the historical ranges of mammals are technically estimations of the present natural ranges (ie a species' potential distribution, in the absence of human modification, given the current climate). The dataset contains estimations of potential contemporary ranges of all mammal species known from the last 130,000 years, and was built under the assumption that humans were primarily responsible for the late Pleistocene megafauna extinction. This assumption seems likely, based on current knowledge (Sandom *et al.* 2014), although debate continues (Cooper *et al.* 2015). Even if humans were responsible for the extinctions near the end of the most recent Ice Age, it seems implausible that extinction patterns for such species should be linked to the contemporary human footprint. We therefore discarded all species from the dataset that were extinct prior to 1500 CE (n = 270). A few species, such as wild horses (*Equus ferus*), went extinct on some continents as part of the megafauna extinction event but survived on others. For similar reasons as the prehistoric extinctions, we adjusted ranges for continentally extirpated species (n = 13). Specifically, if a species went extinct on a continent before 1500 CE, we excluded any portion of the species' range found on that continent (Eurasia was considered as a single continent). The resulting estimates of historical ranges are not strictly bound to any specific time point, and several species, such as the brown bear (*Ursus arctos*), have had slow and continuous range declines in continents where they are still found (Albrecht *et al.* 2017). Given the coarse resolution, it would likely be rare for species to completely disappear from entire grid cell locations while maintaining populations elsewhere within the continent in pre-industrial settings. As such, for the vast majority of species, the reconstructed historical ranges would be expected to be close to their distributions around 1500 CE.

After excluding species and adjusting for prehistoric continental extinctions, we calculated intactness as the ratio of current to historical species richness for each 96.5-km × 96.5-km grid cell location. For example, locations where intactness equaled 1 represent lands where no mammal species extirpations have occurred over the past 500 years; locations where intactness equaled 0.75 maintain 75% of their original species composition; and so forth. We removed pinnipeds, whales, and manatees (94 species) from the analysis by selecting only those species listed in the Phylacine 1.2 database that at least partially occupy terrestrial environments. For our final intactness estimate, we took the natural log of the average body mass (g) of each species (n = 5467); rather than assigning equal weight to each species when calculating species richness, we instead used each of these log values as a weight factor when summing current and historical richness. Body mass data were obtained from the Phylacine 1.2 database (Faurby *et al.* 2018), with input from multiple sources, including Smith *et al.* (2003) and Faurby

and Svenning (2015). Larger-bodied mammals tend to have larger impacts on ecological processes (Morrison *et al.* 2007), lower fecundity rates (Tomiya 2013), and lower population densities (White *et al.* 2007), and we therefore elected to give greater analytical weight to larger species. We used mass-weighted intactness after removing prehistoric extinctions and continental extinctions (alternative intactness metrics are presented in WebFigure 1). For the analysis, we removed pixel locations where historical mammal richness was <15 species, to reduce the possibility of values for single grid cell locations being heavily influenced by small errors in range maps. Performing the analysis using all mapped locations did not result in qualitative changes to the results (WebFigure 2).

After calculating and mapping mammal community intactness, we overlaid this with the human footprint map developed by Venter *et al.* (2016). The human footprint is a composite map based on roads, human population densities, land use, and other features representing the impacts humans have on terrestrial ecosystems. Before overlaying the raster maps, we resampled the human footprint map from 1 km^2 to match the resolution of mammal species intactness (96.5 km^2) using bilinear interpolation, which coarsened the resolution of the data through weighted average of neighboring pixel values. After overlaying mammal species intactness and the resampled human footprint maps, we plotted the values for every grid cell location on a scatterplot and used correlation analysis to evaluate the relationship.

To create bivariate maps combining mammal community intactness and the human footprint, we classified both variables separately into three bins using terciles (three equal-sized groups) of data, with one-third of the locations assigned as "low", one-third as "moderate", and one-third as "high". We then combined these bins into a bivariate classification matrix of nine (three × three) classes, consisting of low human footprint–low mammal community intactness; low human footprint–moderate mammal community intactness; low human footprint–high mammal community intactness; moderate human footprint–low mammal community intactness; moderate human footprint–moderate mammal community intactness; moderate human footprint–high mammal community intactness; high human footprint–low mammal community intactness; high human footprint–moderate mammal community intactness; and high human footprint–high mammal community intactness. We focused our analysis on the four "corners" of this classification (that is, where high or low values intersect along each axis).

To evaluate environmental conditions related to these four situations (ie the corners of the bivariate classification matrix), we calculated summary statistics to produce boxplots from mapped data regarding seven environmental variables, consisting of net primary productivity (NPP; Zhao *et al.* 2005), mean annual temperature (MAT; Fick and Hijmans 2017), mean annual precipitation (MAP; Fick and Hijmans 2017), soil suitability for agriculture based on soil properties and

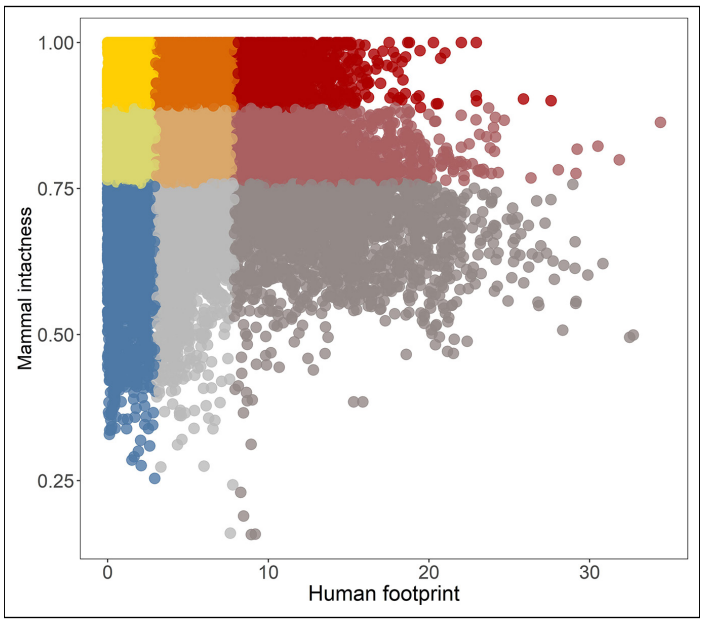

Figure 2. Relationship between the terrestrial human footprint and mammal community intactness for all terrestrial locations on Earth (each point is a 96.5 km resolution mapped pixel location; n = 13,959). Data for each variable were classified into terciles (ie data were split into three equal-sized groups) and combined into nine bivariate classes, represented here by the different colors. Maps of this classification matrix are shown in Figure 3.

climate (Ramankutty *et al.* 2002), elevation and steepness of topography (Fick and Hijmans 2017), and latitude.

We also included the full global dataset (ie all grid cell locations, n = 13,959) in a multiple regression analysis to explore whether the relationship between the human footprint and our estimate of mammal intactness varied with vegetation productivity and between continents. Specifically, we modeled whether mammal community intactness is dependent on a three-way interaction between NPP, continent, and the human footprint using a generalized linear logistic regression approach in R (R Core Team 2018). We investigated the full three-way interaction, as well as the two-way interaction between the human footprint and continent, to explore whether the effects of the human footprint on mammal community intactness differed between continents.

We also assessed whether national economic development levels could possibly explain patterns of mammal community intactness and the human footprint. To do so, we used gross domestic product (GDP) data from the US Central Intelligence Agency's World Factbook (CIA 2016) for each country. We then calculated the average mammal community intactness and human footprint value for each country and plotted country means onto the global scatterplot of mammal community intactness and human footprint, depicting the log of GDP using a color ramp. We also plotted GDP against mean human footprint and mean mammal community intactness and fit linear models to each.

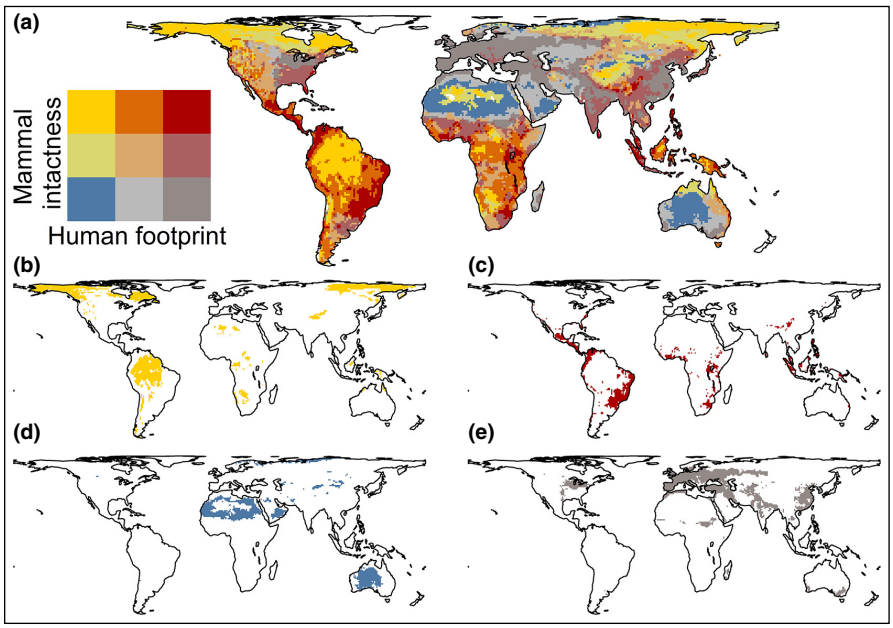

Figure 3. Maps of the bivariate classification using terciles of the human footprint and an index of mammal intactness. The top map (a) shows all nine classes together, while the bottom maps (b–e) show only the four corners of the classification (ie low–high, low–low, high–high, and high–low in scatterplot). (b) Low human footprint–high mammal community intactness (yellow) and (e) high human footprint–low mammal community intactness (gray) represent expected situations based on human impacts on local extirpations; (c) high human footprint–high mammal community intactness (red) and (d) low human footprint–low mammal community intactness (blue) represent unexpected conditions. Maps are projected using WGS 1984 Cylindrical Equal Area.

Both relationships were indistinguishable from zero (R^2 < 0.01; P > 0.54; WebFigure 3).

Results

Mammal community intactness tended to be highest in high-latitude boreal forests and tundra, and low-latitude tropical forests (Figure 1). Globally, mammal community intactness was negatively, albeit not strongly, correlated with human footprint (r = –0.16, P < 0.0001; Figure 2). However, the analysis revealed areas where the human footprint and mammal community intactness were both high (red areas in Figures 2 and 3) and where both were low (blue areas in Figures 2 and 3). Relatively wild areas with both a low human footprint (<2.98, based on tercile breaks) and low mammal community intactness (<0.76) were concentrated in central Australia and the Sahara Desert of Africa. Areas with both a high human footprint (>7.88) and high mammal community intactness (>0.89) were more scattered, occurring in Central America, the Atlantic coast of South America, tropical western and eastern Africa, and parts of Austronesia.

Lands with a low human footprint and high mammal community intactness (yellow locations in Figures 2–4) were environmentally diverse and occurred under widely different climatic conditions (Figures 3 and 4). These wild and intact areas were located mainly in warm tropical or cold boreal regions, but also where soils were less suitable for agriculture (Figure 4). Lands with a low human footprint and low mammal community intactness (blue locations in Figures 2–4) tended to occur in warmer and drier climates, characterized by lower plant productivity and lower agricultural suitability of the soil. Lands with a high human footprint and low mammal community intactness (gray locations in Figures 2–4) were concentrated in higher latitudes, in areas with higher soil suitability for agriculture and intermediate levels of plant productivity. Lands with a high human footprint and high mammal community intactness (red locations in Figures 2–4) were characterized by high levels of plant productivity in relatively warm and wet environments, and with soils that were highly suitable for agriculture. Additional data summarized for all bivariate classes are presented in WebFigure 4.

We found that a three-way interaction between NPP, continent, and human footprint partially explained the variability in mammal community intactness (P < 0.001; R^2 = 0.57). Mammal communities in Africa appear to be less affected by the human footprint than mammals in other continents. The effect of the human footprint depended not only on continent but also on NPP (Figure 5). We plotted the models showing the relationships between human footprint and mammal community intactness for three fixed levels of NPP (lower 20th percentile, median, and upper 80th percentile, which were calculated from the global distribution of NPP values). On most continents, as well as under most levels of NPP, the relationship between human footprint and mammal community intactness was slightly negative (similar to our global correlation analysis). However, in Africa and Australia, the relationship between human footprint and mammal community intactness was unexpectedly positive at low levels of NPP, possibly because human population and NPP may covary on continents with extensive areas of extremely arid conditions (ie large deserts). In North America, higher NPP seems to buffer the effects of the human footprint on mammal community intactness. Across all continents, intactness tended to be higher in areas of higher NPP. Models of the two-way interaction between continent and human footprint are shown in WebFigure 5.

Discussion

The ecological consequences of human impacts are well known, and include elevated risk of species extirpations (Di Marco *et al.* 2018). However, the results of our analysis

suggest that there is not a strong correlation between human activity and the intactness of mammal communities on a global scale. Areas in which high mammal community intactness persists despite a high human footprint may occur because more productive environments support higher population densities of mammals, reducing the risk of local extirpations. Many of these highly productive areas are also identified as global biodiversity hotspots (WebFigure 6; Myers *et al.* 2000; Jenkins *et al.* 2013; Di Marco *et al.* 2018). Although maintaining a relatively high degree of mammal community intactness, these regions are characterized by a human footprint that has increased during the past two decades (Venter *et al.* 2016). Species in these areas could be nearing a threshold beyond which the probability of local extirpations increases non-linearly (Newbold *et al.* 2016), or these areas may represent sites of delayed extinction (eg extinction debts; Kuussaari *et al.* 2009). Efforts to mitigate species losses in these areas should be a high conservation priority.

Regions with a low human footprint and low mammal community intactness were seen primarily in hot, dry regions. Low plant productivity may limit mammal population sizes, and dry conditions may require spatial aggregation of individuals around water resources, making them vulnerable to local extirpations. These arid lands with few roads, sparse human population densities, and minimal land-cover change are characterized by a low degree of human footprint, and have been regarded as relatively wild (Watson *et al.* 2018). Yet their lower degree of mammal community intactness represents ecological degradation driven by human impacts that are difficult to map, such as poaching pressure, invasive species (Woinarski *et al.* 2015), impacts of grazing by domesticated livestock, human appropriation of scarce water resources, or other disruptions to ecological processes or species interactions (Ripple *et al.* 2014).

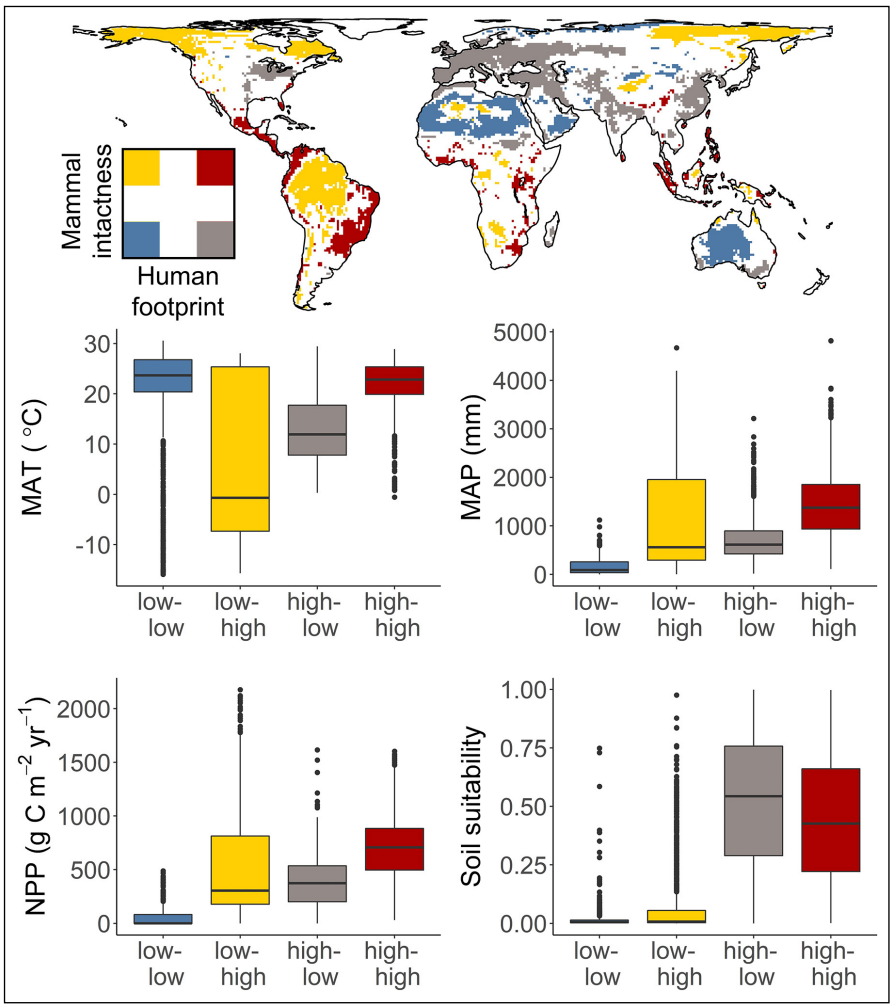

Figure 4. Summaries of variables from the corners of the classification matrix (low–low: low human footprint–low mammal community intactness [blue], n = 1224; low–high: low human footprint–high mammal community intactness [yellow], n = 1902; high–low: high human footprint–low mammal community intactness [gray], n = 1990; and high–high: high human footprint–high mammal community intactness [red], n = 1017, following Figures 2 and 3). MAT: mean annual temperature; MAP: mean annual precipitation; NPP: net primary productivity. Map is projected using WGS 1984 Cylindrical Equal Area. Horizontal lines within boxes depict median values, boxes represent the interquartile range (25th–75th percentiles), whiskers (vertical lines) represent 1.5×interquartile range, and solid circles depict outliers.

The lack of a strong global relationship between human footprint and mammal community intactness provides several important insights into human impacts on nature (Figure 6). First, the impacts of the human footprint on mammal community intactness vary across continents and in different environments. Several locations have endured high levels of human activity but still maintain relatively intact mammal communities. These patterns emerge as a result of complex interactions between climate, ecosystem productivity, the history of human–wildlife interactions, and land use. Uncovering the nature of such patterns and mechanisms will require additional research. Second, the concept of the human footprint could be updated to include estimates of biological intactness. Adding measures of biological intactness to existing human footprint maps would provide an important ecological aspect to identification and prioritization of wildlands for conservation. Other global maps of biological intactness have been developed (Newbold *et al.* 2016), but none of these existing maps have – until now – considered all species within a single taxonomic class (in this case, Mammalia) as a historical baseline for estimating intactness, due to the limited availability of spatial data on the historical distributions of species.

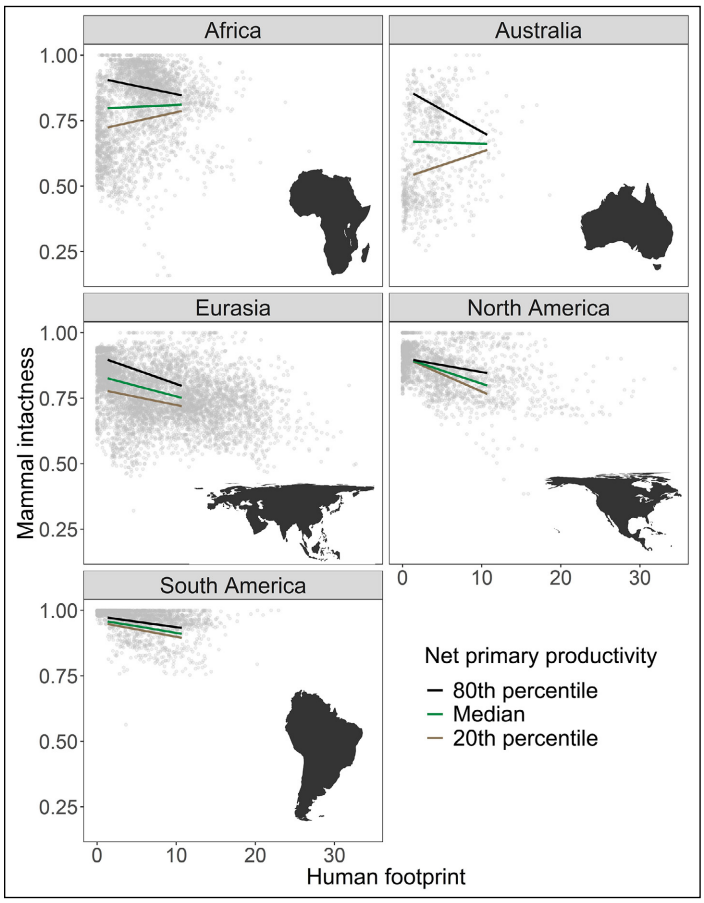

Figure 5. Three-way interaction between the human footprint, NPP, and continent using all grid cell locations (n = 13,959). The effects of the human footprint on mammal community intactness were found to vary among continents (WebFigure 5), but were also dependent on NPP.

Using the human footprint as a means to map the "last of the wild" has provided important insights into wildland conservation priorities (Watson *et al.* 2018). Another important component of wildlands is the relative intactness (or wholeness) of the system's ecological components (Aplet 1999). Including mammal community intactness as a measure of ecological wholeness based on historical references could focus conservation efforts on protecting the least human-modified and most intact landscapes. We consider these sites to be the wildest areas remaining on Earth, based on both the lack of human impact *and* the presence of intact mammal communities (Aplet 1999). Efforts to map the world's remaining wildlands could include our estimate of mammal community intactness to further prioritize global conservation efforts aimed at protecting wilderness areas (Watson *et al.* 2018).

Alternatively, lands with a high human footprint and high mammal community intactness may also be regarded as high priorities for protecting biodiversity and mitigating growing pressures from human development. Hotspots of global biodiversity are well-known conservation priorities (Myers *et al.* 2000), but these areas have increasingly experienced human impacts (Venter *et al.* 2016). Over 41% of the global biodiversity hotspots identified in our analysis are lands with the most intact (ie the top one-third) assemblages of mammal species, even though only slightly more than 5% of global hotspots are among the least human modified (WebFigure 6). Unlike areas with a low human footprint, such human-modified, intact, and critical biodiversity hotspots require greater consideration of social and cultural factors (eg behavioral norms and practices) that mediate human interactions with wildlife. Doing so can reveal which social–ecological mechanisms facilitate coexistence between humans and wildlife (Carter and Linnell 2016).

Any global evaluation of historical and current species presence will include caveats. Notably, the coarse resolution of our mammal distribution maps and the presence of a species within a 96.5-km × 96.5-km grid cell location (a relatively large area) will likely result in overestimation of the habitat currently or historically used by a species. For instance, some species may just have been transient inhabitants of certain locations. This may be especially true in arid regions, where few species permanently inhabit areas mapped as suitable habitat. Moreover, our estimates of mammal community intactness relied only on species presence and not on population densities. Researchers who have recommended measures of species intactness that rely on contemporary references suggest including population estimates in indices (Scholes and Biggs 2005; Newbold *et al.* 2016). Unfortunately, we do not have historical population size estimates for all mammal species.

Conclusions

Our objective here was to explore broad biogeographic patterns between the human footprint and a new estimate of mammal community intactness. In so doing, we discovered unexpected situations across the planet, and call attention to global priorities for protecting wildlands and human-impacted lands that maintain highly intact mammal communities. It may be tempting for conservation biologists to use the human footprint as a coarse proxy for species intactness or ecological integrity, but our results indicate that interactions among these factors are more complex. We suggest that metrics of the human footprint and biological intactness be integrated to create a more comprehensive global measure of ecological integrity, as we have done here. These global metrics not only more fully represent ecological conditions but also reveal new areas of inquiry into the complex relationships between the environment, species composition, and human sociocultural behaviors that impact species.

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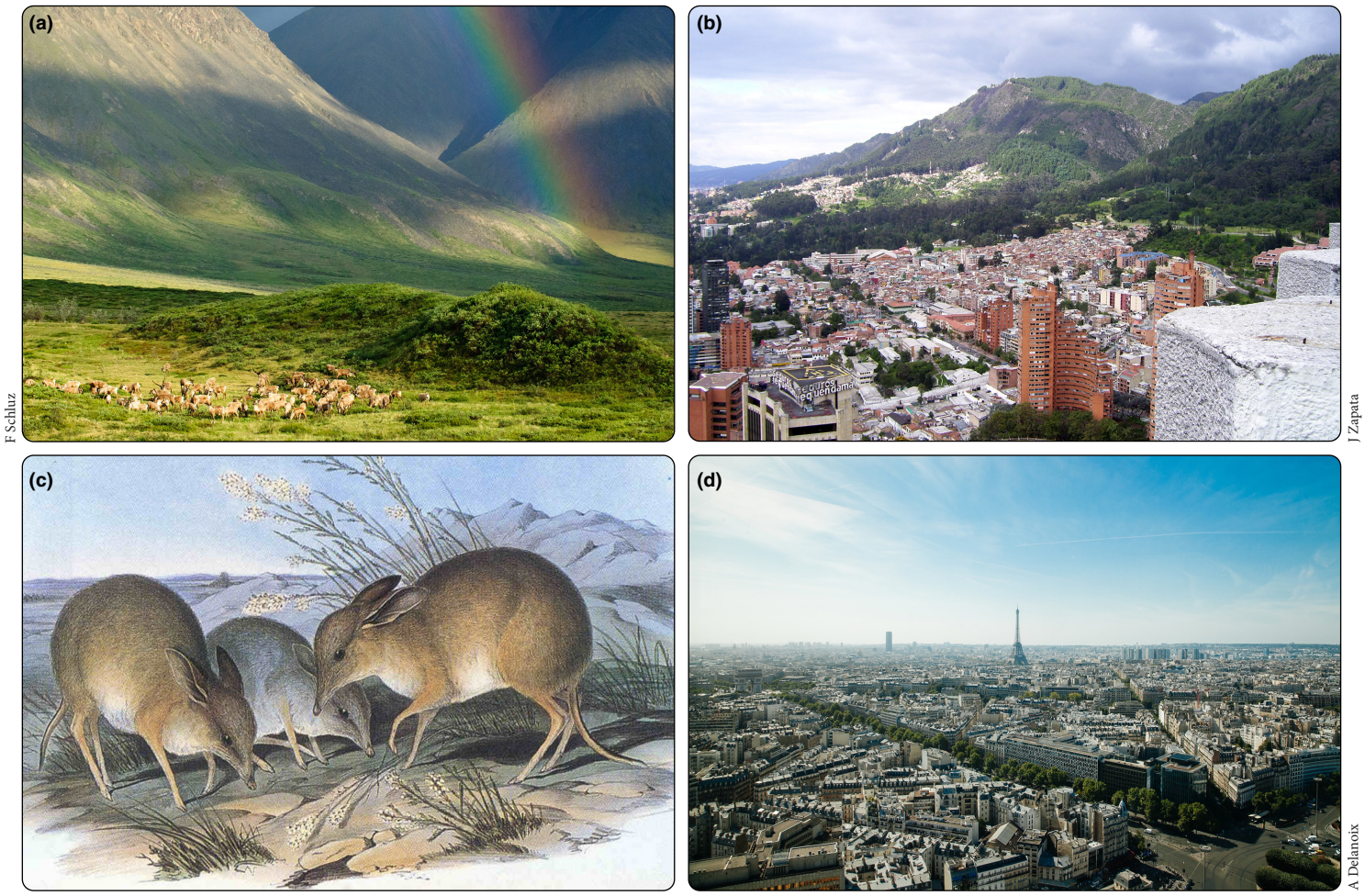

Figure 6. Human impacts and their effects on mammal community intactness differ around the world. Examples of lands characterized by a relatively high human footprint and those with a low human footprint with relatively high or low intactness of mammal species composition relative to historical composition are shown here. (a) The Arctic National Wildlife Refuge in Alaska has experienced a low human footprint and maintains a relatively intact community of mammal species, whereas (b) other areas, such as in Colombia, are characterized by a high human footprint but also maintain a relatively high proportion of their historical composition of mammal species. (c) Areas with a low human footprint, such as Western Australia, have experienced species extirpations (eg the pig-footed bandicoot [*Chaeropus ecaudatus*] shown here) leading to relatively low intactness of mammal communities. (d) Finally, areas with a high human footprint, such as Western Europe, have relatively low mammal community intactness.

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