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# The signature of human pressure history on the biogeography of body mass in tetrapods

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## Abstract

**Aim:** Examining the biogeography of body size is crucial for understanding how animal communities are assembled and maintained. In tetrapods, body size varies predictably with temperature, moisture, productivity seasonality and topographical complexity. Although millennial-scale human pressures are known to have led to the extinction of primarily large-bodied tetrapods, human pressure history is often ignored in studies of body size that focus on extant species. Here, we analyse 11,377 tetrapod species of the Western Hemisphere to test whether millennial-scale human pressures have left an imprint on contemporary body mass distributions throughout the tetrapod clade.

**Location:** Western Hemisphere.

**Time period:** Contemporary.

**Major taxa studied:** Tetrapods (birds, mammals, amphibians and reptiles).

**Methods:** We mapped the distribution of assemblage-level median tetrapod body mass at a resolution of 110 km across the Western Hemisphere. We then generated multivariate models of median body mass as a function of temperature, moisture, productivity seasonality and topographical complexity, as well as two variables capturing the history of human population density and human-induced land conversion over the past 12,000 years. We controlled for both spatial and phylogenetic autocorrelation effects on body mass–environment relationships.

**Results:** Human pressures explain a small but significant portion of geographical variation in median body mass that cannot be explained by ecological constraints alone. Overall, the median body mass of tetrapod assemblages is lower than expected in areas with a longer history of high human population density and land conversion, but there are important differences among tetrapod classes.

**Main conclusions:** At this broad scale, the effect of human pressure history on tetrapod body mass is low relative to that of ecology. However, ignoring spatial variation in the history of human pressure is likely to lead to bias in studies of the present-day functional composition of tetrapod assemblages, at least in areas that have long been influenced by humans.

**KEYWORDS**

Americas, amphibians, body size, functional diversity, human pressure, terrestrial vertebrates, western hemisphere, reptiles

# 1 | INTRODUCTION

Body size is arguably the most important trait of animals, underlying many of their physiological, ecological and evolutionary processes (Peters, 1983; Smith & Lyons, 2013). Since Bergmann (1847) first observed that the distribution of body size across species within an assemblage varies with latitude, geographical patterns in assemblage-level body size have been documented for a multitude of tetrapod taxa (Gouveia & Correia, 2016; Morales-Castilla, Olalla-Tárraga, Purvis, Hawkins, & Rodríguez, 2012; Morales-Castilla, Rodríguez, & Bradford, 2012; Olalla-Tárraga & Rodríguez, 2007; Olson et al., 2009; Rodríguez, Olalla-Tárraga, & Hawkins, 2008). These studies suggest that a small set of ecological constraints – chiefly temperature, moisture, seasonality in productivity and topographical complexity – may be sufficient to explain a large portion of broad-scale variation in the body size of the four terrestrial tetrapod clades (mammals, birds, amphibians and reptiles; Table 1).

Much of our understanding of assemblage-level body size gradients assumes that contemporary species distributions approximate their natural state in the absence of human pressures (Faurby & Svenning, 2015). Nevertheless, humans have contributed to the decline and extinction of many species since the late Pleistocene, and these extinctions have affected certain areas and taxa more than others (Lyons, Smith, & Brown, 2004; Sandom, Faurby, Sandel, & Svenning, 2014). Ignoring the filtering effect of human influence (Balmford, 1996) might lead to bias in biogeographical analyses that rely on inferences from contemporary species distributions (Faurby & Araújo, 2016; Faurby & Svenning, 2015; Santini, González-Suárez, Rondinini, & Di Marco, 2017).

Geographical patterns in the median body size of tetrapod assemblages are particularly likely to display a signal of millennial-scale human pressures (Crees et al., 2016; Faurby & Araújo, 2016) because humans have affected tetrapods of different sizes unevenly (Cardillo et al., 2005; Owens & Bennett, 2000). First, harvesting since the late Pleistocene has disproportionately affected large-bodied species, contributing to the widespread extirpation of megafauna (Lyons et al., 2004; Sandom et al., 2014), especially in mammals and birds, but also reptiles (Slavenko, Tallowin, Itescu, Raia, & Meiri, 2016). Second, human-induced land conversion has contributed to higher declines and extinction risk for larger-bodied tetrapod species, as evidenced in recent decades (Dirzo et al., 2014; Newbold et al., 2013). The common explanation for this is that large-bodied species have smaller population sizes and require larger ranges to survive, making them particularly prone to environmental perturbations (Sodhi, Brook, & Bradshaw,

**TABLE 1** Hypotheses of broad-scale environmental drivers of median body mass variation in tetrapods

| Hypothesis | Variable | Taxon | Relationship with median body mass | | Hypothesis details |
| --- | --- | --- | --- | --- | --- |
| | | | Expected | Modelled | |
| Ecological constraints | | | | | |
| Heat conservation | Temperature | Birds and mammals | − | − | Large body mass is favoured in cold areas owing to higher heat conservation potential (Bergmann, 1847) |
| Heat gain | Temperature | Amphibians and reptiles | + | − | Large body mass is favoured in hot areas owing to higher heat gain potential (Olalla-Tárraga & Rodríguez, 2007) |
| Desiccation | Standard moisture index | Tetrapods | − | − | Large body mass is favoured in dry areas owing to lower desiccation risk (Gouveia & Correia, 2016) |
| Seasonality | Productivity seasonality | Tetrapods | + | + | Large body mass confers higher starvation resistance in seasonal environments (Blackburn et al., 1999) |
| Topographical complexity | Altitude standard deviation | Tetrapods | − | − | Species with large body mass require large ranges and are excluded from areas with high topographical complexity (Rodríguez et al., 2008) |
| Human pressure | | | | | |
| Harvesting | First significant human population density | Tetrapods | − | − | Species with large body mass are disproportionately affected by harvesting (Cardillo et al., 2005; Sandom et al., 2014; Slavenko et al., 2016) |
| Habitat loss | First significant land conversion | Tetrapods | − | − | Species with large body mass suffer higher extinction risk from habitat loss (Cardillo et al., 2005; Dirzo et al., 2014) |

*Note.* Shown are the hypothesized proximal drivers (Hypothesis), the measured proxy variables providing a test of each hypothesis (Variable), the taxonomic scale of each hypothesis (Taxon), the expected and modelled relationships between each variable and assemblage-level median body mass, and details and sources for each hypothesis. Plus and minus signs represent positive and negative relationships, respectively.

2009). Harvesting and land conversion since the late Pleistocene have contributed to the species-level extinction of large-bodied species across the tetrapod clade (Supporting Information Figure S1; see also Slavenko et al., 2016; Smith & Lyons, 2011). Moreover, these human activities have also led to the range contraction of many additional large species, which nonetheless remain extant in areas of lower human pressure (Faurby & Svenning, 2015; Laliberte & Ripple, 2004). Therefore, owing to human-induced extinction and range contraction, we may expect to find a spatial signal of millennial-scale human pressure on the body size distributions of contemporary tetrapod assemblages. Specifically, we hypothesized that median body size would be smaller in areas with a longer history of high human population density and human-induced land conversion (Table 1).

Here, we tested whether human population density and land conversion in the last 12,000 years across the Western Hemisphere underlie, in part, the contemporary variation in tetrapod body size that cannot be explained through ecological constraints alone. We analysed the most complete assemblage-level body mass distributions for tetrapods of the Western Hemisphere, striking a rare balance between taxonomic and spatial breadth. We had the following three main objectives: (a) to document geographical patterns in the median body mass of contemporary tetrapod assemblages of the Western Hemisphere; (b) to test for the effects of millennial-scale human pressures (human population density and human-induced land conversion) on geographical patterns in tetrapod body mass; and (c) to estimate the relative importance of human pressure variables versus ecological factors on body mass distribution. This final test provides insight into how strongly humans have influenced present-day distributions of the functional composition of tetrapods across the Western Hemisphere and whether this signal is consistent among tetrapod classes.

## 2 | METHODS

### 2.1 | Species distributions

We obtained polygon range maps for all extant species of terrestrial tetrapods native to the Western Hemisphere: 3,344 amphibians [International Union for the Conservation of Nature (IUCN), 2016], 4,273 birds (Birdlife International & NatureServe, 2016), 1,751 mammals (IUCN, 2016), and 3,491 reptiles (including squamates, freshwater turtles and crocodilians; IUCN, 2016). Squamate maps for the Caribbean and Central and South America are the result of a recent effort by NatureServe and IUCN to assess the distribution and extinction risk of reptile species in those regions (e.g., Young, 2012). We extracted range maps onto a Behrmann equal area grid with a resolution of 110 km × 110 km (c. 1° at the equator) at the Western Hemisphere extent. We defined unique taxon assemblages as the list of species whose range polygons intersected each grid cell across this grid. Owing to the difficulties of obtaining reliable median estimates from distributions with low sample sizes, we focused on species assemblages with at least 10 species. Furthermore, we excluded coastal cells with < 50% land cover. We derived assemblage species lists for all tetrapods combined and each of the four classes separately.

### 2.2 | Body mass

Despite being susceptible to temporal fluctuations, body mass (in grams) is the most comparable index of body size across taxa that dramatically differ in body shape (Meiri, 2010). We obtained species-level adult body mass data for Western Hemisphere mammals, birds and 95% of reptiles from global compilations (Dunning, 2008; Feldman, Sabath, Pyron, Mayrose, & Meiri, 2016; Myhrvold, Baldridge, Chan, Freeman, & Ernest, 2015; Slavenko et al., 2016; Smith et al., 2003; Wilman et al., 2014; Supporting Information Table 1 in Appendix S1). Body mass information for amphibian species of the Western Hemisphere was derived from the most up-to-date global species-level compilation of amphibian traits (Oliveira, São-Pedro, Santos-Barrera, Penone, & Costa, in review). Although this compilation includes adult body mass data for only c. 7% of Western Hemisphere amphibians, it does include adult body length information (in millimetres) for 74% of these species. Given that amphibians exhibit a strong taxon-specific allometric relationship between body length and body mass (Deichmann, Duellman, & Williamson, 2008), we imputed missing body mass values from available body length information, supplemented by phylogenetic relationships and three ecological traits with > 70% completion rate (foraging strategy, offspring per year and breeding strategy), using the missForest package in R (Stekhoven, 2013; see Supporting Information Appendix S1). We examined the influence of imputation uncertainty on our results by re-running amphibian and tetrapod models after removing amphibian families subject to the highest imputation errors (Supporting Information Appendix S1). Additionally, we used an imputation approach analogous to that for amphibians to derive body mass values for the remaining 5% of reptiles.

We $\log_{10}$-transformed body mass values for all tetrapod species and derived the distribution of logged body mass values for each species assemblage in our study area. From these assemblage-level body mass distributions, we then extracted the median value for all tetrapods combined, as well as for each tetrapod class separately.

Body mass is phylogenetically conserved across tetrapods (Pagel's $\lambda = 0.981$; Supporting Information Table 1 in Appendix S2). As a result, geographical patterns in body mass may arise spuriously because of the phylogenetic non-randomness of species assemblages, rather than environmental filtering on body mass (Lawing, Eronen, Blois, Graham, & Polly, 2017). To address this, we generated phylogenetically standardized median body mass values for each species assemblage (Supporting Information Appendix S2). We obtained phylogenetic information across tetrapods from the timetree of life, a compilation of 2,274 studies representing 50,632 species (Hedges, Marin, Suleski, Paymer, & Kumar, 2015). We used the Generalized Least Squares procedure of Martins and Hansen (1997) implemented in the R package ape (Paradis, Claude, & Strimmer, 2004) to calculate the body mass ancestral reconstruction of each assemblage (Supporting Information Appendix S2). This approach removes the proportion of variation in body mass resulting from the shared phylogenetic component of each assemblage; any residual geographical pattern in this measure would then arise independent of phylogenetic autocorrelation among tetrapod species (Lawing et al., 2017).

After combining distribution, body mass and phylogenetic information, we were able to analyse 11,377 (88% of extant) tetrapod species, including 3,281 amphibians, 3,529 birds, 1,597 mammals and 2,970 reptiles.

## 2.3 | Predictor variables

We obtained data on two human pressure (first significant human population density and first significant land conversion) and four ecological (temperature, moisture, seasonality in productivity and topographical complexity) predictor variables (Table 1) and aggregated all spatial data at a 110 km × 110 km grid cell resolution (Supporting Information Figure S2).

We obtained first significant human population density and first significant land conversion from the History Database of the Global Environment (HYDE version 3.1; Klein Goldewijk, Beusen, Van Drecht, & De Vos, 2011) dataset, which includes spatially explicit data on human-induced global land-use changes over the past 12,000 years. We calculated first significant human population density as the year before present in which the mean human population density of each grid cell exceeded one inhabitant per 100 $km^2$. This threshold reflects expected median population density estimates for big-game hunting populations of Clovis groups (Prasciunas & Surovell, 2015; Waguespack & Surovell, 2003). We assumed the influence on tetrapod populations to be minimal for human population densities below this threshold. We calculated first significant land conversion as the year before present in which the combined cover of cropland, pasture and urban in each grid cell exceeded 20% (Ellis et al., 2013). Cells where human population density and land conversion currently remain below their respective thresholds were assigned a value of zero.

We downloaded annual mean temperature (in degrees Celsius) and annual mean climate moisture index data from the CliMond Archive (v1.2; Kriticos et al., 2012) as 1961–1990 averages for the entire globe. We obtained data on seasonality in productivity from Coops, Waring, Wulder, Pidgeon, and Radeloff (2009), who calculated the annual coefficient of variation in the fraction of visible light (photosynthetically active radiation) absorbed (fPAR; an index of vegetation canopy greenness) from MODIS data. We calculated topographical complexity as the standard deviation in altitude across all 1-km grid cells included within each 110 km × 110 km grid cell using data from the Shuttle Radar Topography Mission (SRTM30; Farr et al., 2007).

We calculated variance inflation factors (VIF) to estimate collinearity among the six predictor variables. VIFs ranged between 1.12 and 2.79, indicating very low collinearity among variables (Fox, 2002), so we kept all six variables in our statistical analyses.

## 2.4 | Statistical analyses

We quantified the additive effects of the four ecological and two human pressure predictor variables on median body mass using multivariate ordinary least square (OLS) models for all tetrapods combined and separately for each tetrapod class. We generated separate models for observed and phylogenetically standardized median body mass

responses. To facilitate interpretation of the relative importance of model coefficients, we standardized all predictors by subtracting the mean and dividing by two standard deviations (Gelman, 2008).

OLS model residuals across all taxa were subject to high spatial autocorrelation, as estimated using Moran's *I* correlograms (Supporting Information Figures 1 and 2 in Appendix S3). To avoid issues of statistical non-independence resulting from high spatial autocorrelation, we used the method of principal coordinates of neighborhood matrices (PCNM; Borcard & Legendre, 2002). This approach involves performing a principal coordinates analysis on the distance matrix expressing the spatial relationship among all grid cells. Eigenvectors generated using this approach represent independent spatial filters, which can be included as spatial predictor variables within multivariate models and, thus, easily incorporated within a multimodel inference framework (Diniz-Filho, Rangel, & Bini, 2008). To avoid overfitting body mass variation in each taxon, we selected the subset of 9–28 spatial filters that reduced the Moran's *I* of the first distance class below 0.1 (Supporting Information Appendix S3). Calculation and selection of spatial filters was done using SAM (Spatial Analysis in Macroecology) v4.0 (Rangel, Diniz-Filho, & Bini, 2010).

For each median body mass response in turn, we first generated the maximal OLS model including all ecological and human pressure predictors plus spatial filters. We then generated all potential simplifications of this maximal model that also included all spatial filters. The simplest model we considered was thus a model including an intercept plus a slope for each spatial filter. We ranked all candidate models using the Akaike information criterion (AIC; Burnham & Anderson, 2002) and quantified the relative weight of evidence for each model using AIC weights ($AIC_w$). For responses where no single model was overwhelmingly supported (i.e. $AIC_w \geq 0.9$), we considered the model set comprising all models with Akaike weights within at least 5% of the best model weight (Coyle & Hurlbert, 2016; Supporting Information Table 1 in Appendix S4). Based on this best model set (Supporting Information Appendix S4), we used the R package MuMIn (Barton, 2015) to calculate model-averaged coefficients and confidence intervals for each predictor appearing at least once. Coefficients for each predictor were averaged only over the models in which the predictors appeared. We also quantified the proportion of all models in the best model set containing each predictor as a further indication of variable importance (Burnham & Anderson, 2002).

For each taxon, we determined the relative contribution of ecological, human pressure and spatial predictors to body mass variation using variance partitioning (Legendre & Legendre, 1998), as implemented in the *varpart* R function in 'vegan' (Oksanen et al., 2016). This approach estimates the individual contribution to body mass variation of each predictor set, as well as the shared contribution of each combination of predictor sets, once all other predictors have been accounted for. Given the different number of predictors in each set, we interpreted individual and shared contributions to variance using $R^2$ values adjusted for sample size. In addition, we assessed whether individual contributions from each predictor set represented a significant proportion of explained median body mass variation. We did so by comparing the

observed individual contribution of each predictor set to its individual contribution on 1,000 random permutations of the median body mass response, and calculating a *p*-value (Peres-Neto, Legendre, Dray, & Borcard, 2006).

Finally, we examined how predictions of tetrapod median body mass varied spatially across the Western Hemisphere when variation in human pressure variables was considered or ignored. We used the full model including all predictors to predict the median body mass in each grid cell based on the following: (a) spatial variation in all predictors (ecological, human pressure and spatial); and (b) spatial variation in all predictors except human pressure variables (which were kept constant at their mean value). Comparing these two sets of spatial predictions with observed body mass values enabled us to identify areas where disregarding human pressure led to higher prediction errors.

## 3 | RESULTS

The median body mass of tetrapod assemblages displays a strong latitudinal gradient across the Western Hemisphere, increasing towards the poles (Figure 1a; Supporting Information Figure 1 in Appendix S2). This tetrapod pattern largely mirrors those of birds and mammals (Figure 1b,c; Supporting Information Figure 1b,c in Appendix S2; see also Blackburn & Gaston, 1996; Rodríguez et al., 2008), which are the two tetrapod classes with the highest number of widely distributed species. Birds and mammals have a median range area of 56 and 34 grid cells, respectively, compared with four and two grid cells for reptiles and amphibians. Moreover, amphibian and reptile assemblages with at least 10 species (our cut-off value for analyses) are particularly rare at higher latitudes. Therefore, bird and mammal distributions drive the positive latitudinal body-mass gradient we find across tetrapods. In contrast, amphibians and reptiles individually do not display this latitudinal gradient and instead exhibit a discordant longitudinal relationship, particularly in North America (Figure 1d,e; Supporting Information Figure 1d,e in Appendix S2; see also Olalla-Tárraga & Rodríguez, 2007; Olalla-Tárraga, Rodríguez, & Hawkins, 2006).

The combination of ecological and human pressure variables in our models, together with the spatial filters included to minimize residual spatial autocorrelation, explain 82% of the variation in tetrapod median body mass (explained variation in phylogenetically standardized median body mass is 90%; Supporting Information Figure 3 in Appendix 2). Among tetrapod classes, mammals are the best explained (82–88%), whereas amphibians are the least well explained (48–49%).

Ecological effects on tetrapod body mass are mostly congruent with expectations, with the notable exception of the negative effect of temperature on body mass in both amphibians and reptiles (Table 1; Figure 2; Figure 2 in Supporting Information Appendix S2). The most important ecological constraint (as determined by its standardized model-averaged regression coefficient) differs among taxa. Temperature is the strongest predictor for all tetrapods combined, birds and mammals; moisture, seasonality and topography are the most important predictors for amphibians and reptiles.

Human pressure explains variation in tetrapod body mass that cannot be explained by ecological and spatial predictors alone. Historical human population density and land conversion are consistently selected in the best models of median body mass (Figure 2; Supporting Information Figure 2 in Appendix S2; Supporting Information Appendix S4). Overall, the median body mass of tetrapod assemblages is lower in cells with a longer history of high human population density and human-induced land conversion (Figure 2a; Supporting Information Figure 2a in Appendix S2). Furthermore, ignoring variation in human pressure leads to less accurate predictions of body mass across many areas with a long history of human pressure (i.e., areas in the top 25% of significant human population density or land conversion history; Figure 3). Nevertheless, despite being significant across tetrapods, the proportion of median body mass variance explained solely by human pressure predictors is very small compared with the individual proportions explained by ecological and spatial predictors (Figure 4; see also Supporting Information Figure S3; Figure 3 in Supporting Information Appendix S2). The unique contribution of human pressure increases (but remains considerably smaller than that of ecology) across areas with a longer history of human pressure (Figure 4b). Moreover, the influence of human pressure on median body mass is particularly low in amphibians and reptiles. Counter to our tetrapod-level expectations, the signal that we do detect in these taxa indicates a slight positive association between median body mass and human pressure history (Figure 2a; Supporting Information Figure 2 in Appendix S2).

## 4 | DISCUSSION

Anthropogenic activities have had substantial impacts on biodiversity and ecosystem structure throughout the Holocene (Malhi et al., 2016). These impacts should be considered in analyses of contemporary biogeographical patterns that rely on geographical range estimates no more than a few hundred years old (Crees et al., 2016). We have shown that sustained human pressures should be considered alongside ecological constraints when examining contemporary biogeographical patterns of body mass across the tetrapod clade, at least in regions where humans have been present for multiple millennia.

When data on all tetrapods are combined, we find that millennial-scale human pressures explain additional spatial variation in median body mass that cannot be explained by ecological constraints alone. Specifically, observed body mass across tetrapods is generally lower in areas with a longer history of significant human population density and land conversion. Predicting body mass in these regions based solely on ecological constraints often results in an overestimation of median tetrapod body mass. This finding supports evidence that human modifications of species' geographical ranges have truncated the upper tail of body mass frequency distributions in mammals (Faurby & Araújo, 2016; Santini et al., 2017; Smith & Lyons, 2011) and indicates that a comparable signature is detectable at the tetrapod level. In addition, the inclusion of human pressure predictors also improves prediction of median tetrapod body mass in a number of high-latitude regions that
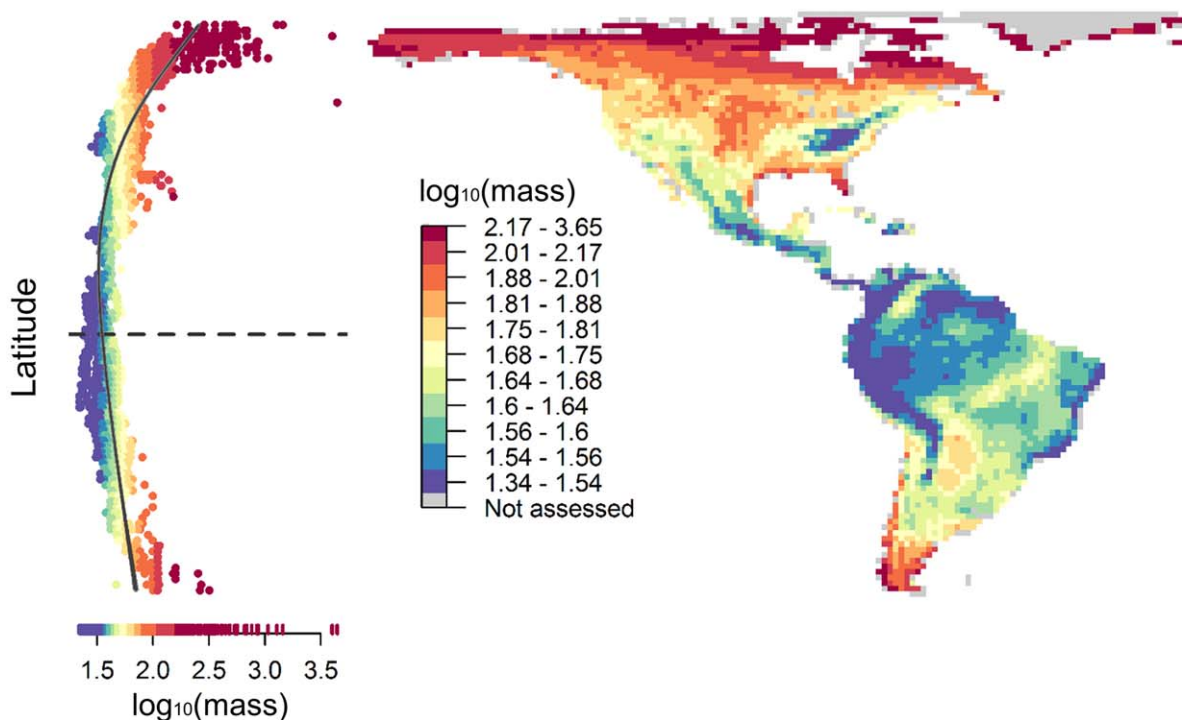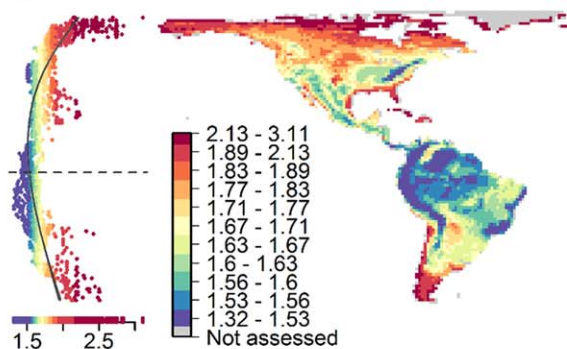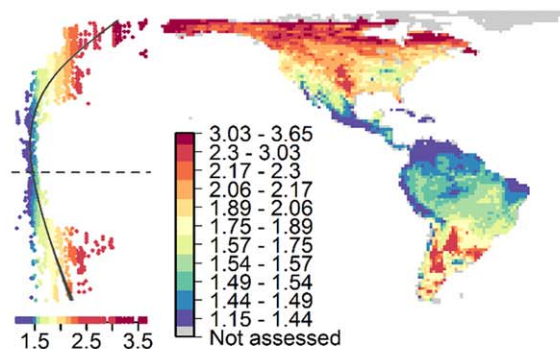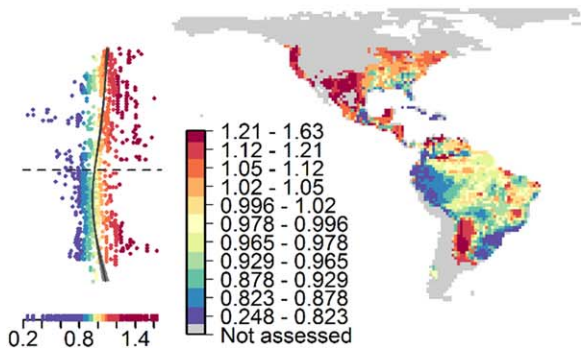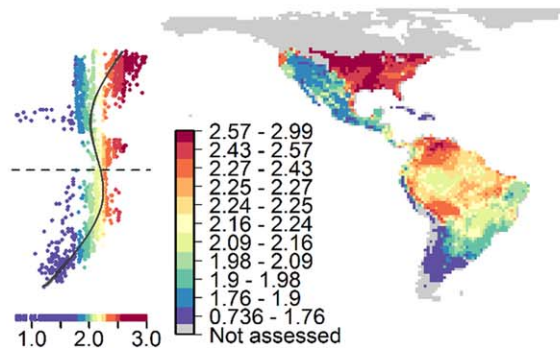
**FIGURE 1** Geographical distribution of median body mass across Western Hemisphere tetrapods. Mapped values represent the $\log_{10}$ median body mass (in grams) of the assemblage corresponding to each 110 km × 110 km grid cell. Scatter plots to the left of each panel indicate the scatter of all grid cells across latitude, with the dashed horizontal line representing the equator and the continuous line representing a natural cubic spline through the scatter points. Colours in the scatter plot correspond to those in the maps. Grid cells in light grey were not assessed because they included < 10 species for the corresponding taxon
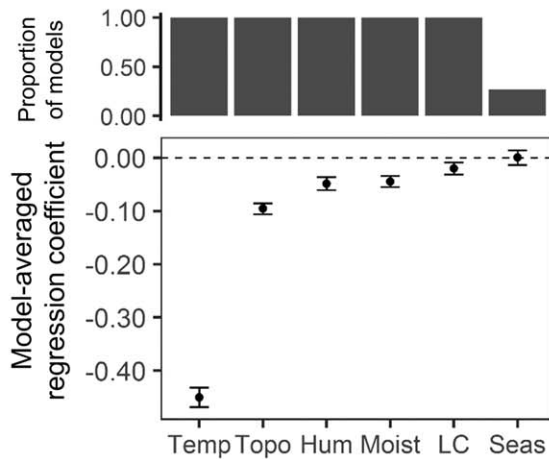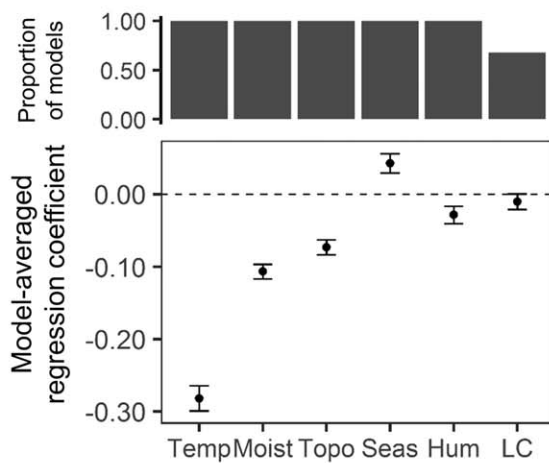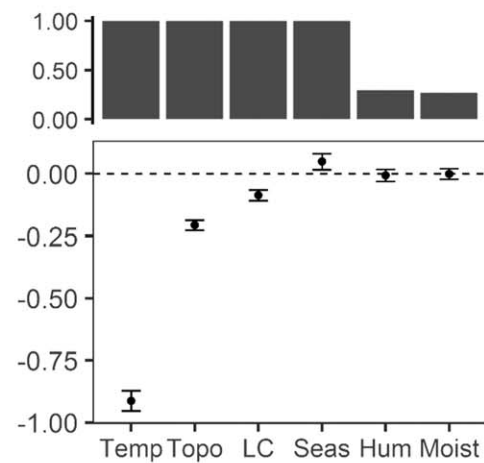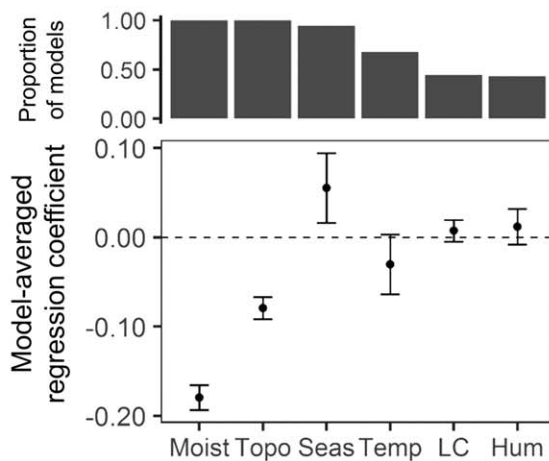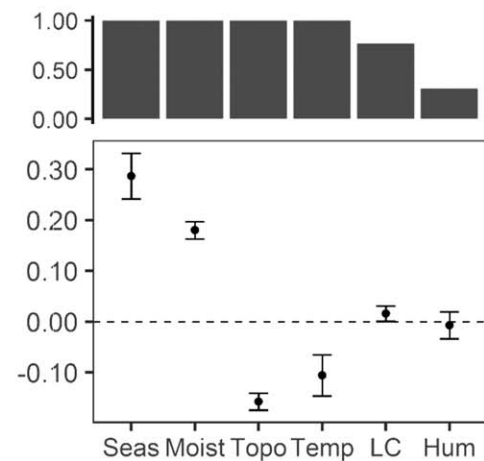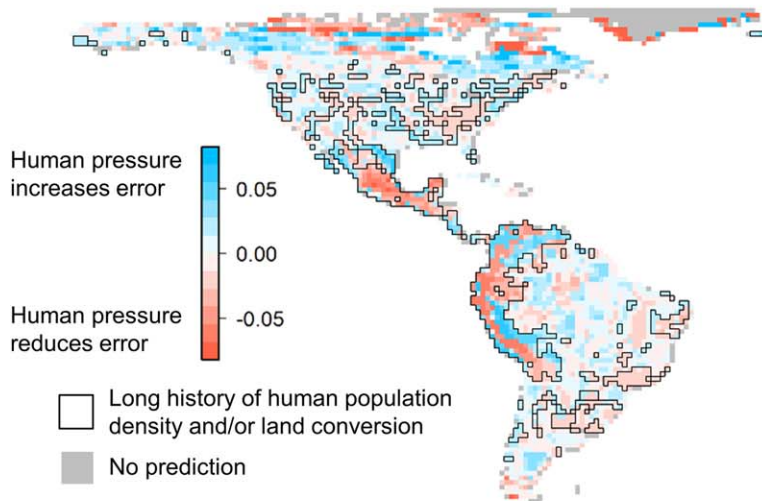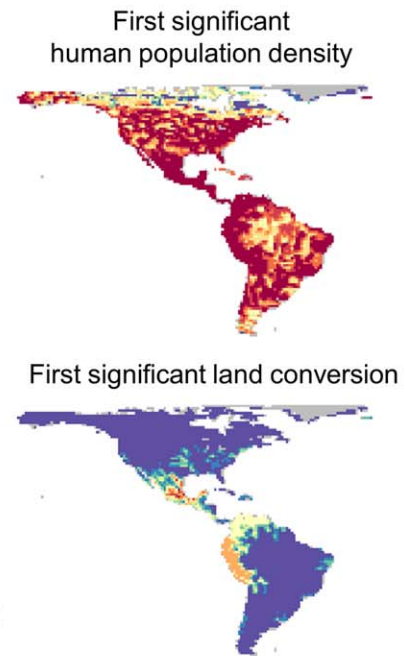
**FIGURE 2** Model-averaged regression (β) coefficients for six predictors of variation in median body mass across tetrapods. Values represent standardized coefficients, such that higher absolute coefficients suggest a stronger effect. Histograms at the top of each panel indicate the number of models in the best predictor set that contained each predictor. All models in the best model set used for model averaging also included all selected spatial filters aimed at accounting for spatial autocorrelation in model residuals (Supporting Information Appendix S3). Error bars represent 95% confidence intervals for each coefficient. Hum = first significant human population density; LC = first significant land conversion; Moist = mean annual moisture index; Seas = seasonality in productivity; Temp = mean annual temperature; Topo = altitude standard deviation

## a) Prediction errors



Human pressure increases error — 0.05

0.00

Human pressure reduces error — -0.05

☐ Long history of human population density and/or land conversion

▨ No prediction

## b) Human pressure predictors

First significant human population density

First significant land conversion

## c) Ecological predictors

Annual mean temperature

Annual mean moisture index

Seasonality in productivity
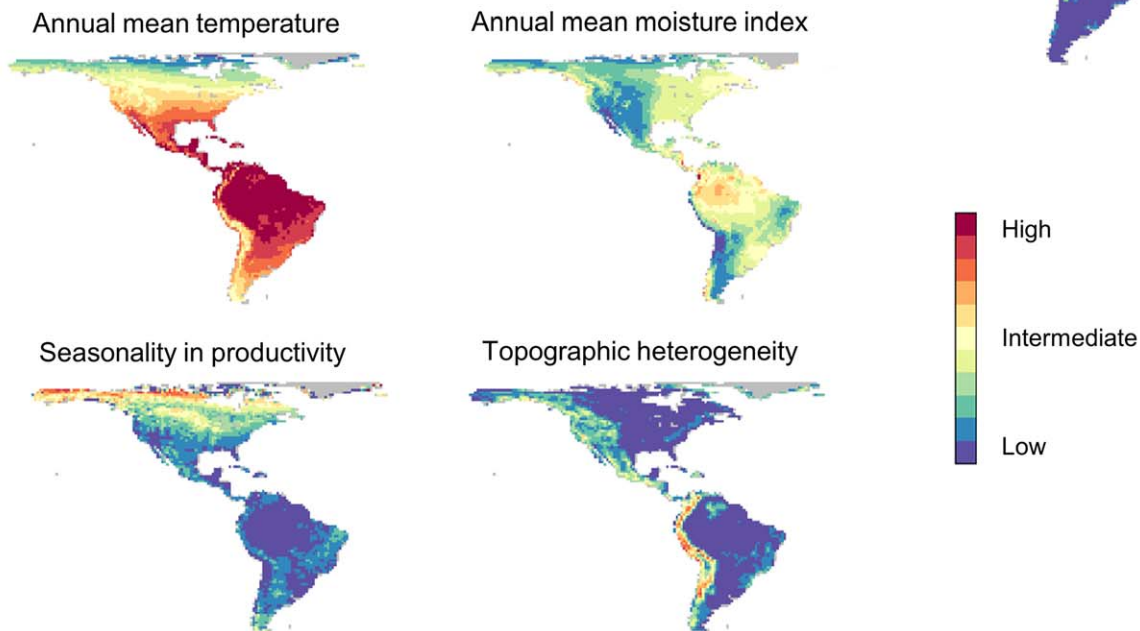
Topographic heterogeneity

High

Intermediate

Low

**FIGURE 3** Comparison of median tetrapod body mass prediction errors between models considering or ignoring variation in human pressure predictors. (a) Map of differences in absolute prediction errors (i.e., predicted minus observed median body mass) between models accounting for ecological predictors alone or in addition to human pressure predictors. Both models also included spatial filters to account for spatial autocorrelation (Supporting Information Appendix S3). The black polygon encompasses grid cells in the top 25% of either first significant human population density or first significant land conversion. Light grey indicates terrestrial cells not included in our statistical analyses. (b) Maps of human pressure predictors used in the models. (c) Maps of ecological predictors used in the models. The colour scale in the bottom right corner applies to all maps in (b) and (c)

have not been strongly influenced by humans (see Figure 3a). Contrary to areas with a long history of human pressure, models based on ecological constraints alone tend to underestimate body mass in these regions, a potential consequence of weakened associations between contemporary body mass distributions and their environment (e.g., Faurby & Araújo, 2016; Santini et al., 2017). Therefore, human pressure predictors may also present a way to adjust estimates of the

relationships between body mass and ecological variables of interest, such as temperature or moisture.

There are three primary ways in which humans may have influenced tetrapod body mass distributions in the late Pleistocene and throughout the Holocene: hunting, habitat alteration and translocations (Koch & Barnosky, 2006). All three of these human drivers are likely to have impacted larger-bodied tetrapod species disproportionately
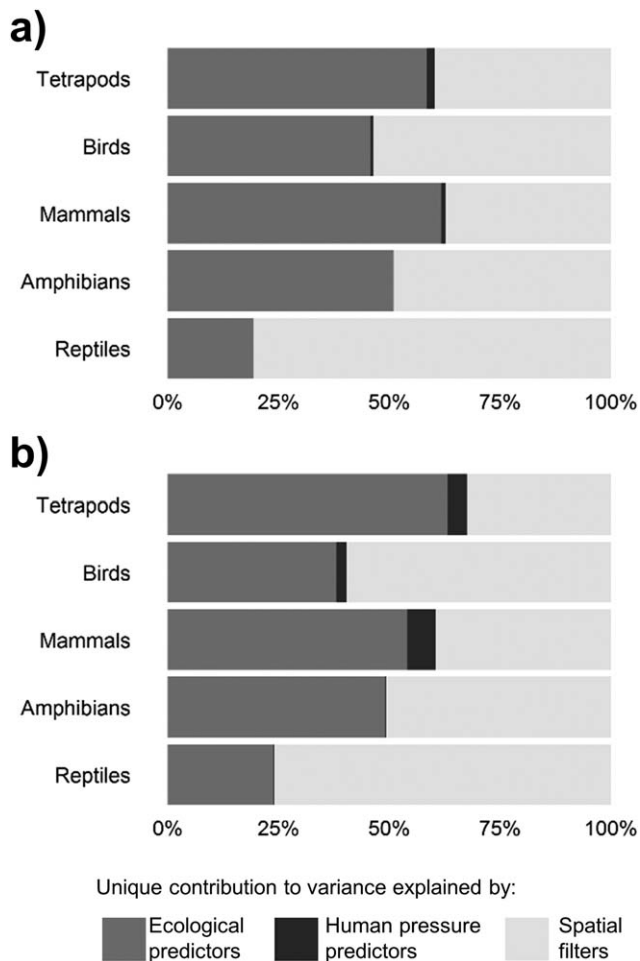
**FIGURE 4** Relative percentage of explained tetrapod median body mass variance solely contributed to by ecological, human pressure and spatial filter variables. Shown are the relative unique contributions to total body mass variance explained (a) across the whole Western Hemisphere and (b) across grid cells in the top 25% of either first significant human population density or first significant land conversion. Unique contributions were derived from variance partitioning and represent the coefficients of determination (adjusted $R^2$) for the individual (non-shared) contribution of each predictor set. Here, these unique contributions are expressed as relative percentages of total variance explained. For the full variance partitioning results, see Supporting Information Figure S3

through population declines, range contractions and extinctions (Dirzo et al., 2014; Grayson, 2001; Koch & Barnosky, 2006; Pimm, Raven, Peterson, Şekercioğlu, & Ehrlich, 2006). First, because larger species provide a higher return, heavy human hunting pressure is likely to have driven more rapid declines in larger than smaller vertebrate prey populations (Grayson, 2001). The depletion of larger prey populations is reflected in the archeological record through the appearance of additional prey items and an overall decrease in the size of prey in the human diet (Grayson, 2001). Dwarfing as a consequence of the increased survival of smaller individuals may also reflect the long-term influence of hunting pressure on body mass in a number of taxa (e.g., bison; McDonald, 1981). Second, habitat alteration in the form of land

clearing, deforestation or altered fire regimes may also have disproportionately affected large-bodied tetrapods (Crees et al., 2016; Fritz, Bininda-Emonds, & Purvis, 2009), which have lower population densities and require larger ranges to survive (Sodhi et al., 2009). Third, there is a long history of human-mediated translocation of species dating back to the late Pleistocene (Boivin et al., 2016), including the intentional or inadvertent introduction of predators (e.g., rats, dogs) and virulent diseases (Boivin et al., 2016; Grayson, 2001; Koch & Barnosky, 2006). These introductions have previously been linked with the extinction of megafauna on islands (e.g., New Zealand; Holdaway, 1999), but could theoretically also have played a role on continents (Prowse, Johnson, Bradshaw, & Brook, 2014).

Beyond the tetrapod-level signal, we find notable differences in the magnitude and direction of human pressure effects among tetrapod classes (see Figure 4). These differences may reflect the varying effects of human pressure drivers on body mass distributions across tetrapod classes. The magnitude of human pressure effects is highest in mammals and birds, and it is consistent with tetrapod-level patterns. Such a high signal in mammals and birds is expected, given that most of the nearly 800 mammal and bird global species-level extinctions documented in the last 12,000 years are likely to have been at least partly driven by human factors (Crees et al., 2016; Koch & Barnosky, 2006; Pimm et al., 2006; Sandom et al., 2014). Indeed, previous studies also indicate a signature of human pressure history on mammal body mass comparable to the one we present here (Faurby & Araújo, 2016; Fritz et al., 2009; Santini et al., 2017). In contrast, the effect of human pressure history on contemporary amphibian and reptile body mass is minimal and incongruent with our expectations; there is a weak increase in median body mass with first significant human population density and land conversion in amphibians and reptiles, respectively. These effects may indicate that millennial-scale human pressures have had a higher influence on the lower than the upper tail of body mass frequency distributions in amphibians and reptiles. One potential reason for this could be that the major impact of humans on these taxa has been to drive declines in small-ranged endemics (Manne, Brooks, & Pimm, 1999), which are disproportionately small-bodied (Gaston & Blackburn, 1996), for instance, through land conversion to agriculture (González-Suárez, Gómez, & Revilla, 2013). Moreover, this could indicate good adaptability of larger-bodied amphibians and reptiles to human-modified environments (Suazo-Ortuno et al., 2015; Vilela, Villalobos, Rodríguez, & Terribile, 2014). On the whole, the differences we find among tetrapod classes indicate that general conclusions on the consequences of past and ongoing human pressure on contemporary macroecological patterns based on a single taxon (e.g., mammals) may not apply fully across all tetrapods.

Nevertheless, our study indicates that the spatial signal arising from the human-driven range contraction of large-bodied extant species is weak across the Western Hemisphere, especially when compared with the signal of ecological variables. The low explanatory power of human pressure is likely to stem from the fact that contemporary distribution data for extant tetrapods do not consider Pleistocene species-level extinctions, which were disproportionately of large-

bodied species (Supporting Information Figure S1). Instead, this suggests that millennial-scale human pressures may already have filtered out the vast majority of large-bodied species sensitive to anthropogenic activities through species-level extinction (Faurby & Araújo, 2016; Faurby & Svenning, 2015). In particular, this filtering effect may be responsible for the apparent discrepancy between previous size-biased extinctions in reptiles (see Supporting Information Figure S1) and the human pressure signature on contemporary median body mass in this taxon (see Figure 2); this discrepancy suggests that the influence of human pressure on tetrapod body mass is multifaceted, and its assemblage-level effect may vary over time. A full exploration of the impacts of human pressure history will require incorporation of the Paleontological record to estimate the ranges of extinct tetrapods (e.g., Faurby & Svenning, 2015; Sandom et al., 2014) and testing for the effect of removal of these ranges on ecological and human drivers of body size variation. Nonetheless, our analyses demonstrate that examining variation in contemporary body mass distributions along a coarse gradient of human pressure history does reveal a significant, albeit weak, signal of human influence. This approach can thus be used to expose useful patterns even when more costly and prohibitive extinct species' range reconstructions are unavailable.

Our analysis of nearly 90% of extant tetrapod species in the Western Hemisphere also shows that a small set of ecological constraints explain up to 70% of the variation in tetrapod-level median body mass. Birds and mammals largely drive results at the tetrapod level, because those classes have more broad-ranged and high-latitude species than amphibians and reptiles. Consistent with expectations (Table 1), body mass in mammals and birds increases with latitude (i.e., Bergmann's rule; Bergmann, 1847) and decreases with annual mean temperature, annual mean moisture and topographical complexity, with temperature being much the strongest predictor. These results agree with previous studies of the biogeography of mammal and bird body size (Morales-Castilla, Olalla-Tárraga, et al., 2012; Olson et al., 2009).

In contrast, amphibians and reptiles display different and more complex geographical patterns in body mass. Neither class displays a strong latitudinal cline, instead showing substantial longitudinal variation (e.g., from the tropical Andes to the Atlantic coast in amphibians and from western to eastern North America in reptiles). These patterns reflect the stronger effect of moisture (amphibian body mass decreases and reptile body mass increases with moisture) relative to temperature (see also Gouveia & Correia, 2016; Olalla-Tárraga et al., 2006). In addition, the effect of seasonality in productivity is much higher in amphibians and reptiles than in birds and mammals, potentially indicating that the higher susceptibility of smaller-bodied species to starvation in highly seasonal environments (Blackburn, Gaston, & Loder, 1999) represents a stronger constraint in ectotherms than endotherms. Counter to expectations, we found that body mass decreased slightly with temperature in reptiles and amphibians (Table 1). The effect of temperature on ectotherms is likely to depend on taxon-specific differences in behavioural thermoregulation (Olalla-Tárraga & Rodríguez, 2007). In reptiles, for instance, we found that the sign of the temperature effect changed to the expected positive relationship when removing

freshwater turtles and crocodilians (78 species; Supporting Information Figure S5). Most freshwater turtle species in our dataset are large and inhabit higher latitudes, probably driving the negative relationship between body mass and temperature when all reptiles are combined. These results indicate that a more complete understanding of the effects of temperature on body mass in ectotherms will require a more detailed analysis that considers variation across phylogenetic scale.

The present findings are subject to two main sources of uncertainty, stemming from the taxonomic and geographical breadth of our study. First, we recognize that the imputations of body mass for amphibians were subject to substantial error. However, removing amphibian species from families prone to imputation error had virtually no effect on tetrapod-level patterns (median body mass was 99% correlated; Supporting Information Appendix S1). In amphibians, removing uncertain species led to very minor quantitative geographical differences that did not translate into qualitative differences in environmental relationships (Supporting Information Appendix S1). For these reasons, we do not believe that our main conclusions are significantly affected by the imputation of a large portion of body mass values in amphibians.

Second, previous studies have also highlighted the importance of regional history, in terms of both evolutionary and biogeographical history, in determining geographical patterns in assemblage-level body size (Morales-Castilla, Olalla-Tárraga, et al., 2012; Morales-Castilla, Rodríguez, et al., 2012). Although we did not explicitly incorporate biogeographical history in our models, we accounted in part for evolutionary history by calculating phylogenetically standardized median body mass responses. We found no major qualitative differences in broad-scale spatial patterns between unstandardized and phylogenetically standardized median body mass (Supporting Information Appendix S2). However, our analyses are not sufficient to assess the role of evolutionary history on contemporary patterns of tetrapod body mass, which will require the incorporation of information on major historical events, such as biotic interchanges (Morales-Castilla, Olalla-Tárraga, et al., 2012). Moreover, the significant proportion of variance explained by spatial filters suggests that additional spatial processes, possibly related to evolutionary and biogeographical history, remain to be accounted for in our models.

## 5 | CONCLUSION

Overall, our study reveals a significant albeit weak signature of human pressure history on the contemporary biogeography of body mass across Western Hemisphere tetrapods. Our results corroborate previous findings based on mammals (Faurby & Araújo, 2016; Fritz et al., 2009; Santini et al., 2017). Therefore, we reaffirm the need to integrate anthropogenic variables in studies of contemporary macroecological patterns. However, our study also highlights important differences in the direction and magnitude of human pressure effects among tetrapod classes, occasionally counter to expectations. These differences are key, as they indicate that conclusions based on one class (e.g., mammals) need not apply across all tetrapods. Further elucidation of

how multiple past and ongoing human pressures have influenced the functional composition of different tetrapod taxa will be crucial in the face of increasing anthropogenic pressures.

## REFERENCES

Balmford, A. (1996). Extinction filters and current resilience: The significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution*, 5347, 193–196.

Barton, K. (2015). *MuMIn: Multi-model inference. R package version 1.15.1*.

Bergmann, C. (1847). Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gottinger Studien*, 3, 595–708.

Birdlife International & NatureServe. (2016). *Bird species distribution maps of the world*. Cambridge, U.K. and Arlington, VA.

Blackburn, T. M., & Gaston, K. J. (1996). Spatial patterns in the body sizes of bird species in the New World. *Oikos*, 77, 436–446.

Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: A clarification of Bergmann's rule. *Diversity and Distributions*, 5, 165–174.

Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M., … Petraglia, M. D. (2016). Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences USA*, 113, 6388–6396.

Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 153, 51–68.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York: Springer.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., & Sechrest, W. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, 309, 1239–1242.

Coops, N. C., Waring, R. H., Wulder, M. A., Pidgeon, A. M., & Radeloff, V. C. (2009). Bird diversity: A predictable function of satellite-derived estimates of seasonal variation in canopy light absorbance across the United States. *Journal of Biogeography*, 36, 905–918.

Coyle, J. R., & Hurlbert, A. H. (2016). Environmental optimality, not heterogeneity, drives regional and local species richness in lichen epiphytes. *Global Ecology and Biogeography*, 25, 406–417.

Crees, J. J., Carbone, C., Sommer, R. S., Benecke, N., Turvey, S. T., & Crees, J. J. (2016). Millennial-scale faunal record reveals differential resilience of European large mammals to human impacts across the Holocene. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152152.

Deichmann, J. L., Duellman, W. E., & Williamson, G. B. (2008). Predicting biomass from snout–vent length in new world frogs. *Journal of Herpetology*, 42, 238–245.

Diniz-Filho, J. A. F., Rangel, T. F. L. V. B., & Bini, L. M. (2008). Model selection and information theory in geographical ecology. *Global Ecology and Biogeography*, 17, 479–488.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.

Dunning, J. B. Jr. (2008). *Body masses of birds of the world*. Boca Raton, FL: CRC Press.

Ellis, E. C., Kaplan, J. O., Fuller, D. Q., Vavrus, S., Goldewijk, K. K., Verburg, P. H., … Verburg, P. H. (2013). Used planet: A global history. *Proceedings of the National Academy of Sciences USA*, 110, 7978–7985.

Farr, T., Rosen, P., Caro, E., Crippen, R., Duren, R., Hensley, S., … Alsdorf, D. (2007). The shuttle radar topography mission. *Reviews of Geophysics*, 45, 1–33.

Faurby, S., & Araújo, M. B. (2016). Anthropogenic impacts weaken Bergmann's rule. *Ecography*, 39, 1–2.

Faurby, S., & Svenning, J. C. (2015). Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Diversity and Distributions*, 21, 1155–1166.

Feldman, A., Sabath, N., Pyron, R. A., Mayrose, I., & Meiri, S. (2016). Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecology and Biogeography*, 25, 187–197.

Fox, J. (2002). *An R and S-Plus companion to applied regression*. Thousands Oaks, CA: Sage.

Fritz, S. A., Bininda-Emonds, O. R. P., & Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. *Ecology Letters*, 12, 538–549.

Gaston, K. J., & Blackburn, T. M. (1996). Range size–body size relationships: Evidence of scale dependence. *Oikos*, 75, 479–485.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, 27, 2865–2873.

González-Suárez, M., Gómez, A., & Revilla, E. (2013). Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes. *Ecosphere*, 4, art76.

Gouveia, S. F., & Correia, I. (2016). Geographical clines of body size in terrestrial amphibians: Water conservation hypothesis revisited. *Journal of Biogeography*, 43, 1–10.

Grayson, D. K. (2001). The archaeological record of human impacts on animal populations. *Journal of World Prehistory*, 15, 1–68.

Hedges, S. B., Marin, J., Suleski, M., Paymer, M., & Kumar, S. (2015). Tree of life reveals clock-like speciation and diversification. *Molecular Biology and Evolution*, 32, 835–845.

Holdaway, R. N. (1999). Introduced predators and avifaunal extinction in New Zealand. In R. D. E. MacPhee (Ed.), *Extinctions in near time: Causes, contexts, and consequences* (pp. 189–238). Boston, MA: Springer.

International Union for Conservation of Nature (IUCN). (2016). *The IUCN red list of threatened species*. http://www.iucnredlist.org. Downloaded on 08 February 2016

Klein Goldewijk, K., Beusen, A., Van Drecht, G., & De Vos, M. (2011). The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography*, 20, 73–86.

Koch, P. L., & Barnosky, A. D. (2006). Late quaternary extinctions: State of the debate. *Annual Review of Ecology, Evolution, and Systematics*, 37, 215–250.

Kriticos, D. J., Webber, B. L., Leriche, A., Ota, N., Macadam, I., Bathols, J., & Scott, J. K. (2012). CliMond: Global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods in Ecology and Evolution*, 3, 53–64.

Laliberte, A. S., & Ripple, W. J. (2004). Range contractions of North American carnivores and ungulates. *BioScience*, 54, 123.

Lawing, A. M., Eronen, J. T., Blois, J. L., Graham, C. H., & Polly, P. D. (2017). Community functional trait composition at the continental scale: The effects of non-ecological processes. *Ecography*, 40, 651–663.

Legendre, P., & Legendre, P. (1998). *Numerical ecology* (2nd English ed.). Amsterdam, The Netherlands: Elsevier Science BV.

Lyons, S. K., Smith, F. A., & Brown, J. H. (2004). Of mice, mastodons and men: Human-mediated extinctions on four continents. *Evolutionary Ecology Research*, 6, 339–358.

Malhi, Y., Doughty, C. E., Galetti, M., Smith, F. A., Svenning, J.-C., & Terborgh, J. W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences USA*, 113, 838–846.

Manne, L. L., Brooks, T. M., & Pimm, S. L. (1999). Relative risk of extinction of passerine birds on continents and islands. *Nature*, 399, 258–261.

Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, 149, 646–667.

McDonald, J. (1981). *North American bison: Their classification and evolution*. Berkeley, CA University of California Press.

Meiri, S. (2010). Length–weight allometries in lizards. *Journal of Zoology*, 281, 218–226.

Morales-Castilla, I., Olalla-Tárraga, M. Á., Purvis, A., Hawkins, B. A., & Rodríguez, M. Á. (2012). The imprint of cenozoic migrations and evolutionary history on the biogeographic gradient of body size in New World mammals. *The American Naturalist*, 180, 246–256.

Morales-Castilla, I., Rodríguez, M. Á., & Bradford, A. (2012). Deep phylogeny, net primary productivity, and the global bird body size gradient. *Biological Journal of the Linnean Society*, 106, 880–892.

Myhrvold, N. P., Baldridge, E., Chan, B., Freeman, D. L., & Ernest, S. K. M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109.

Newbold, T., Scharlemann, J. P. W., Butchart, S. H. M., Şekercioğlu, Ç. H., Alkemade, R., Booth, H., & Purves, D. W. (2013). Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20122131.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Dan McGlinn, P., . . . Wagner, H. (2016). *vegan: Community Ecology Package. R package version 2.4–0*.

Olalla-Tárraga, M. Á., & Rodríguez, M. Á. (2007). Energy and interspecific body size patterns of amphibian faunas in Europe and North America: Anurans follow Bergmann's rule, urodeles its converse. *Global Ecology and Biogeography*, 16, 606–617.

Olalla-Tárraga, M. Á., Rodríguez, M. Á., & Hawkins, B. A. (2006). Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography*, 33, 781–793.

Oliveira, B. F., São-Pedro, V. A., Santos-Barrera, G., Penone, C., & Costa, G. C. AmphiBIO: A global database for amphibians ecological traits. *in review*.

Olson, V. A., Davies, R. G., Orme, C. D. L., Thomas, G. H., Meiri, S., Blackburn, T. M., . . . Bennett, P. M. (2009). Global biogeography and ecology of body size in birds. *Ecology Letters*, 12, 249–259.

Owens, I. P., & Bennett, P. M. (2000). Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences USA*, 97, 12144–12148.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, 87, 2614–2625.

Peters, R. H. (1983). *The ecological implications of body size*. Cambridge, U.K.: Cambridge University Press.

Pimm, S., Raven, P., Peterson, A., Şekercioğlu, Ç. H., & Ehrlich, P. R. (2006). Human impacts on the rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of Sciences USA*, 103, 10941–10946.

Prasciunas, M., & Surovell, T. (2015). Reevaluating the duration of Clovis: The problem of non-representative radiocarbon. In A. Smallwood & T. Jennings (Eds.), *Clovis: On the edge of a new understanding* (pp. 21–35). College Station, TX: Texas A&M Press.

Prowse, T. A. A., Johnson, C. N., Bradshaw, C. J. A., & Brook, B. W. (2014). An ecological regime shift resulting from disrupted predator–prey interactions in Holocene Australia. *Ecology*, 95, 693–702.

Rangel, T. F., Diniz-Filho, J. A. F., & Bini, L. M. (2010). SAM: A comprehensive application for Spatial Analysis in Macroecology. *Ecography*, 33, 46–50.

Rodríguez, M. Á., Olalla-Tárraga, M. Á., & Hawkins, B. A. (2008). Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Global Ecology and Biogeography*, 17, 274–283.

Sandom, C., Faurby, S., Sandel, B., & Svenning, J.-C. (2014). Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133254.

Santini, L., González-Suárez, M., Rondinini, C., & Di Marco, M. (2017). Shifting baseline in macroecology? Unraveling the influence of human impact on mammalian body mass. *Diversity and Distributions*, 23, 640–69.

Slavenko, A., Tallowin, O. J. S., Itescu, Y., Raia, P., & Meiri, S. (2016). Late Quaternary reptile extinctions: Size matters, insularity dominates. *Global Ecology and Biogeography*, 25, 1308–1320.

Smith, F. A., & Lyons, S. K. (2011). How big should a mammal be? A macroecological look at mammalian body size over space and time. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 2364–2378.

Smith, F. A., & Lyons, S. K. (2013). *Animal body size: Linking pattern and process across space, time, and taxonomic group*. Chicago, IL: University of Chicago Press.

Smith, F. A., Lyons, S. K., Ernest, S. K. M., Jones, K. E., Kaufman, D. M., Dayan, T., . . . Haskell, J. P. (2003). Body mass of Late Quaternary mammals. *Ecology*, 84, 3403.

Sodhi, N. S., Brook, B. W., & Bradshaw, C. J. (2009). Causes and consequences of species extinctions. *The Princeton Guide to Ecology*, 1, 514–520.

Stekhoven, D. R. J. (2013). *missForest: Nonparametric missing value imputation using random forest*. R package version 1.4.

Suazo-Ortuno, I., Alvarado-Diaz, J., Mendoza, E., Lopez-Toledo, L., Lara-Uribe, N., Marquez-Camargo, C., ... Rangel-Orozco, J. D. (2015). High resilience of herpetofaunal communities in a human-modified tropical dry forest landscape in western Mexico. *Tropical Conservation Science*, 8, 396–423.

Vilela, B., Villalobos, F., Rodríguez, M. Á., & Terribile, L. C. (2014). Body size, extinction risk and knowledge bias in new world snakes. *PLoS One*, 9, 3–10.

Waguespack, N., & Surovell, T. (2003). Clovis hunting strategies, or how to make out on plentiful resources. *American Antiquity*, 68, 333–352.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027.

Young, B. E. (2012). Red listing Central American squamates. *Herpetological Review*, 43, 368–370.

## BIOSKETCH

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## SUPPORTING INFORMATION

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