Human pressures filter out the less resilient demographic strategies in natural populations of plants and animals worldwide

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Abstract

The exponential growth that has characterised human societies since the industrial revolution has fundamentally modified our surroundings. Examples include rapid increases in agricultural fields, now accounting for 37% of the land surface, as well as increases in urban areas, projected to triple worldwide by 2030. As such, understanding how species have adapted to and will respond to increasing human pressures is of key importance. Resilience, the ability of an ecological system to resist, recover, and even benefit from disturbances, is a key concept in this regard. Here, using a recently develop comparative demographic framework, we examine how the inherent ability of 921 natural populations of 279 plants and 45 animal species worldwide to respond to disturbances correlates with human settlement size and human activities. We develop a spatially and phylogenetically explicit model parameterised with life history traits and metrics of demographic resilience using the open-access COMPADRE and COMADRE databases, coupled with high-resolution human impact information via the Human Footprint database. We expected: (H1) species' populations located nearer urban areas to have a greater ability to resist, recover, or benefit from human-related disturbances compared to pristine habitats; (H2) human effects on the responses of animal populations to disturbances to depend on the species' ability for long-distance mobility; and (H3): human pressures to constrain the repertoire of life history strategies of animal and plant species via their effects on underlying vital rates and life history traits. We find that: (1) urban areas host a limited diversity of strategies that achieve demographic resilience with, on average, more resistant and faster-recovery populations located near human activities than in pristine habitats; (2) species with limited mobility tend to be more strongly affected by human activities than those with long-distance mobility; and (3) human pressures correlate with a limited set of vital rates and life history traits, including the ability to shrink, and reproduce earlier. Our results provide a

tangible picture of how, having drastically transformed terrestrial landscapes, humans have shaped the ways animals and plants respond to disturbances.

Keywords: amplification, comparative biology, life history trait, life history strategy, phylogenetic analysis, recovery, resistance.

The exponential growth that has characterised human societies since the industrial revolution has fundamentally modified our surroundings[1–5]. Examples include rapid increases in agricultural fields, now accounting for 37% of the land surface[6]. Similarly, urban areas are projected to triple by 2030[7]. Recently, 59% of the Earth's terrestrial surface has been estimated to be under direct, negative impacts by human land use[8]. Such human impacts are resulting in the rapid decrease of species' ranges[9,10]. Examples include the 80% projected decline of black spruce (*Abies nigra*) range in France[11,12], or the forecasted 30% habitat loss for snow leopards (*Panthera unica*) in the Himalaya[13], both by 2010. Ultimately, these fast reductions in species ranges affect the broad macroecological dynamics that regulate life on Earth[14]. Indeed, anthropogenic stressors on ecological systems are responsible for extinction rates comparable to those that caused the Big Five mass extinctions[15,16]. Of these stressors, human settlement size and human activities are strong predictors of species' geographic ranges[17,18], as well as extinction rates in mammals[19], birds[20], and plants[21].

The outcomes of human settlement size and activities on the viability of natural populations can be directly quantified using proxies of human impacts on the target species' demographic schedules. Changes in a natural population's vital rates (e.g., survival, development, reproduction, recruitment) will ultimately shape its success or failure, thus the presence/absence of a species at a given location and its overall range[22–24]. As such, demographic approaches provide us with powerful means to examine population responses to human disturbances[25,26]. Indeed, extensive evidence exists that disturbances shape species' life history strategies (*i.e.*, schedules of vital rates along a species' life cycle[27]), and that these strategies in turn determine the viability of natural populations[28].

In recent decades, life history theory has developed frameworks to quantify and classify species responses to a/biotic disturbances using life history traits from across the Tree of Life. These life history traits, attributes that together describe life history strategies (e.g., generation

time, time at maturity, degree of parity), ultimately impact the performance of a population. Some examples of these frameworks include the r/K strategies[29], the Competition-Stress Tolerator-Ruderal (CSR)[30], the fast-slow continuum[31], and the parity continuum[32]. The fast-slow continuum, in particular, classifies organisms according to a trade-off between allocation to survival *vs.* development. Short-lived, fast-growing species are located at one end of this continuum (e.g. the white trillium, *Trillium grandiflorum*; voles, *Microtus*[32,33]), while extremely long-lived, slow-growing species are found at the opposite end (e.g., the California redwood, *Sequoia sempervirens*; the African bush elephant, *Loxondota africana*[32,33]). The parity continuum, instead organises schedules of reproduction according to allocation into an offspring quality *vs.* quantity trade-off[31,34], and between semelparous *vs.* iteroparous species[32]. Recent work classifying species along the fast-slow and parity continua has revealed that short-lived, semelparous species of plants and animals have the inherent ability to recover faster from natural disturbances[35–37]. Yet, which specific life history strategies are better poised to resist and recover from human impacts remains unknown.

Here, we examine how the ability of 921 natural populations of 279 plants and 45 animal species worldwide (Fig. S1) to respond to disturbances correlates with human settlement size and human activities. Specifically, we build a spatially and phylogenetically explicit model parameterised with life history traits and metrics of demographic resilience using the open-access COMPADRE[38] and COMADRE [39] databases, coupled with high-resolution human impact information via the Human Footprint database[40]. We expected: (H1) species' populations located nearer urban areas to have a greater ability to resist, recover, or even benefit from human-related disturbances compared to those living in more pristine habitats, assuming that the human pressures would have allowed these populations to adapt to frequent disturbance regimes and/or filter out the least resilient ones; (H2) human effects on the responses of animal populations to disturbances to depend on the species' ability for long-distance mobility, but for

these effects to be stronger in low-mobility animal, as their populations cannot flee away from human disturbances; and (H3): human pressures to constrain the repertoire of life history strategies of animal and plant species via their effects on underlying vital rates and life history traits. We find that (1) urban areas host a limited diversity of strategies that achieve demographic resilience with, on average, more resistant and faster-recovery populations located near human activities than in pristine habitats. Interestingly, this pattern also includes a decline in the ability of opportunist species to grow in population size after disturbances when their populations are located close to human settlements. This finding suggests that human urbanisation and land transformation have happened at a far-too-quick rate for resilient strategies to human impacts to have evolved; (2) species with limited mobility, tend to be more strongly affected by human activities than those with long-distance mobility; and (3) human pressures correlate with s limited set of vital rates and life history traits. For instance, individuals of populations located closer to human settlements tend to decrease in size more frequently (*i.e.*, shrinkage) and live faster (*i.e.*, reproduce earlier) than in pristine habitats. This finding is in agreement with recent research that has demonstrated that shrinkage and early maturation are key strategies to persist in suboptimal environments[24,41].

Results

Human impacts on terrestrial habitats are aligned along two independent axes: one of human activities and another one of land usage. To link the main kinds of human impacts and activities on terrestrial habitats to the life history traits and resilience of natural populations, we reduced the dimensionality of the eight components of the Human Footprint[40] using a Principal Component Analysis (PCA). This analysis reveals two dominant axes of variation in human activities, which together explain 53% of the variance (Fig. 1). The first axis, which absorbs 35.86% of this variance, informs on human presence, as it mainly separates areas according to human population density, degree of built environment, and light pollution. The second axis,

125 absorbing 16.63%, describes land use, as it predominantly separates extensive pastures from
126 intense agricultural croplands.

127 To quantify the resilience of the 921 natural populations of our 324 examined species,
128 we adopted a novel framework that classifies populations' inherent abilities to respond to
129 disturbances using transient (*i.e.,* short-term) dynamics[42]. According to this framework, a
130 population's intrinsic resilience can be quantified as per its resistance, speed of recovery, and
131 compensation to shocks (*i.e.* sudden increase in population size after a disturbance)[43]. Next, we
132 predicted these three dimensions of demographic resilience using the two principal component
133 axes of human activities described above via (i) a spatially and phylogenetically explicit model,
134 and also (ii) linear models. The former models allowed us to explicitly consider spatial and
135 phylogenetic autocorrelations, while also estimating the role of phylogenetic inertia in our
136 observed patterns. Our proxy to phylogenetic inertia, Pagel's λ[44], was relatively high with the
137 resistance metrics both for plant (λ = 0.958, $P < 0.001$) and animals (λ = 0.936, $P < 0.001$). It
138 was also high for the two other components of demographic resilience (see Table S4).

139 The demographic resilience of plant and animal populations differ in their association
140 with human activities. Our analyses reveal that animal populations tend to be more resistant (t-
141 test$_{df=107}$= 2.357, P = 0.020) (Fig. 2a; Table S5) than plants when found closer to humans (t-
142 test$_{df=788}$= 1.508, P = 0.132). On the contrary, animal populations exhibit a lower resistance in
143 intense agricultural areas (t_{107}= -3.872, $P < 0.001$), while plant population resistance is not
144 affected by agricultural land use. The speed of recovery to disturbances in plant populations
145 located near human presence is greater than in pristine habitats (t_{788}= 2.976, P = 0.003). While
146 the speed of recovery of animal populations is faster than plants ($t_{112.46}$= 4.35, $P < 0.001$), this
147 demographic resilience component is independent of proximity to human presence for animals.
148 Interestingly, according to phylogenetically informed models, resistance decreases for plant
149 populations closer to human areas ($P_{MCMC} < 0.010$) but it increases for animal closer to humans

(P_{MCMC} = 0.030) and to intensely cultivated areas (P_{MCMC} = 0.010). Regarding the ability of populations to increase in size after a disturbance, plants tend to lose compensation potential close to human presence (P_{MCMC} = 0.010, Fig. 2e), but their compensation remains unaffected by agricultural land use (Fig. 2f). The compensation of animals is not affected by either axis of human activities (Fig. 2e-f).

To test holistically how human presence affects the full demographic resilience portfolio of different species, we used convex hulls[45]. The volume defined by resistance and speed of recovery becomes thinner at higher values of human presence (Fig. 3a). This finding suggests a loss of diversity of the resistance/speed to recovery space in highly urban areas. Along the human presence axis, populations of animals and plants that are closer to human settlements are significantly more resistant (t_{913}= 2.098, P = 0.036, Fig. 2a) and borderline faster at recovering from disturbances (t_{913}= 1.597, P = 0.111, Fig. 2c), while their ability to increase in size after a disturbance is unaffected (t_{913}= -1.342, P = 0.180, Fig. 2e). These results are not in opposition with our previous finding that highly resilient species are not found in highly populated areas; rather they suggest that human presence might not only affect the mean resilience values near human activities but also constrain their variance. This process would then lead to the homogenisation of the resilience dynamics of urban populations.

Simulations of resilience components using convex hulls demonstrate that our reported findings above are indeed linked to human presence. The resulting four-dimensional framework –of which we here show the dimensions of resistance, speed of recovery, and human presence axis for display restrictions (Fig. 3a)– is significantly different from a normal, uniform, or gamma distributions (Fig. 3b). Indeed, the volume occupied by the quantified resistance, speed of recovery, and compensation of our 921 populations as a function of their proximity to human settlements is smaller than that expected under a uniform (observed volume ≈ 0.20 simulated volume, Monte Carlo test with $P < 0.050$), gamma (observed volume ≈ simulated volume, $P <$

175 0.050) or normal distributions of traits ($P < 0.050$). Even when the volume is similar, the space
176 occupied by our data's convex hull differs from the one occupied by the data simulated under
177 the other three kinds of distributions, further emphasising that we are not in a situation where
178 the populations are not affected by the human presence and might have been distributed along
179 this axis uniformly or a situation where a central value would have been preferred. In other
180 words, human presence matter in the distribution of resilience strategies. Overall, this finding
181 suggests that the resilience space of our 921 natural populations of animals and plants may have
182 been eroded by human activities. It is also worth noting that certain combinations of resistance-
183 recovery strategies do not exist (or were not sampled) in our data. Examples include populations
184 with low resistance but high recovery in pristine habitats.

185 The ability to flee from areas with human activities is a key driver of the demographic
186 resilience of animals to human pressures. To test our second hypothesis (H2), that the ability to
187 flee from stress will shape human activities ~ resilience relationships, we re-examined the
188 spatially and phylogenetically explicit models above, this time comparing species with high
189 mobility (*i.e.,* individuals move > 100 Km in their ranges, e.g., *Bonasa umbellus* (ruffed
190 grouse), *Falco naumanni* (lesser kestrel)) *vs.* those with low mobility (< 100 km; e.g., *Emydura*
191 *macquarii* (Macquarie turtle)). Animal species with both strategies, high *vs.* low mobility, gain
192 resistance closer to human presence ($t_{34} = 2.510$, $P = 0.017$; $t_{71} = 1.954$, $P = 0.055$; respectively),
193 but this enhanced resistance is more pronounced for low mobility species (Fig. 4a). Along the
194 axis of agricultural land use, both groups show a decrease in resistance in intense agricultural
195 lands, though this decline is sharper for high ($t_{71} = -2.362$, $P = 0.021$) than for low mobility
196 species ($t_{34} = -4.964$, $P < 0.001$; Fig. 4b). However, when taking into account spatial and
197 phylogenetic relationships, the populations of low mobility animal species are more resistant
198 along the axis of agricultural land use ($P_{MCMC} = 0.040$) and that the resistance of both high and
199 low mobility species is independent of human presence. For the speed of recovery and

200 compensation, only low mobility species respond –and only mildly so– by recovering faster
201 (t_{34}= 1.916, P = 0.064, Fig. 4c) and compensating more (t_{34} = 1.971, P = 0.057, Fig. 4e) the
202 closer they are to human presence, and by compensating more (t_{34} = -2.374, P = 0.023, Fig. 4f)
203 and being more resistant (t_{34} = -4.694, P < 0.001, Fig. 4b) when closer to agriculturally intensive
204 areas. However, under our spatially and phylogenetically explicit model, the speed of recovery
205 and compensation appear to not be affected by the two axes of human pressure in neither of the
206 two groups of animal species (Table S5-6).

207 Human pressure effects of species demographic resilience are modulated via their
208 impacts on only a limited set of vital rates and life history traits. To test hypothesis H3, that
209 human pressures will correlate with changes in underlying vital rates and life history strategies,
210 we developed a spatially and phylogenetically explicit model that accounts for adult body mass
211 (for animals) or maximum height (for plants), separately (See Methods and Supplementary
212 Online Materials). Surprisingly, the vital rates structuring our populations are not significantly
213 affected by the effects of human presence, agricultural land use, nor their interaction (Table 1a).
214 A notable exception is the ability of plants to shrink from one year to the next, which is
215 positively correlated with both axes of human activities. In our pool of plant species, individuals
216 in populations closer to human-transformed habitats tend to shrink more than those in pristine
217 habitats. This finding is in agreement with studies that have shown that plant shrinkage
218 increases chances of survival[46], likely through the cut down in respiratory demands[47], and a
219 recent work showing that plant populations persist in unsuitable environments thanks to their
220 ability to shrink[24]. Indeed, plant populations closer to human presence have slightly higher
221 survival rates than in pristine habitats. Similarly, life history traits linked to reproduction are
222 not affected by human pressures (Table 1b). Most life history traits do not respond to human
223 pressures, except for generation time in animals, which tends towards a slight increase closer
224 to human settlements (Table 1b). Further analyses, where animal species are separated based

225 on their high *vs.* low mobility, show that generation time is significantly longer in animal
226 populations with high mobility that are primarily located closer to both human presence or in
227 more intense agricultural lands ($P_{MCMC} < 0.050$), while this life history trait is not affected in
228 low-mobility animal species (see Table S5-6). However, amongst low mobility animals, age at
229 first reproduction decreases significantly when their populations are located close to human
230 presence and intensive agriculture ($P_{MCMC} < 0.050$).

231

232 **Discussion**

233 Using a novel framework that quantifies and compares components of demographic
234 resilience across vastly different species[43], we show how human presence and human activities
235 have shaped –and especially constrained– the repertoire of demographic resilience strategies
236 across 921 populations from 326 animal and plant species worldwide. Our findings also
237 highlight how species that lack the ability for long-distance mobility/migration are more deeply
238 impacted by human activities. The employed demographic resilience framework illustrates how
239 human pressure affects a key aspect of demography: a populations ability to resist, recover, and
240 even, in some cases, grow after a disturbance. Our convex hulls show a clear thinning of the
241 resilience hypervolume of natural populations in urban habitats compared to pristine
242 ecosystems. Closer to human settlements and intense agricultural areas, we report species with
243 greater degrees of resistance and recovery time, but a narrow range of resilience. This finding
244 in highly anthropised areas supports the hypothesis of abiotic homogenisation of resilience traits
245 with intense human pressures[48,49]. Together, our findings suggest that human activities have
246 filtered out less resilience species.

247 Species with a low potential of demographic resilience are found in pristine habitats,
248 but not in urban places. This finding suggests that low-resilience species cannot persist in

249 human environments characterized by intense, frequent disturbances. An alternative
250 explanation for this pattern is that low-resilience species might not have been present in areas
251 where humans have settled and transformed the land. Indeed, humans have mostly settled in
252 places with a high primary production and relatively stable climates[50]. However, these
253 locations, by offering conditions that are not too extreme and relatively stable hence, should
254 have selected for species with adaptations to disturbances. Indeed, resilience strategies to
255 disturbances often come at a cost to organisms, which thus can be too expensive to persist in
256 environments where they are not that frequently used[51]. Consequently, maintaining some
257 resistance aspect would be done at the expense of some other functions, leading to a reduced
258 competitive ability in stable environments[52]. Furthermore, here we have worked only under the
259 prism of the outcomes of human activities and infrastructures. It is possible that key social
260 aspects of human societies as well as natural disturbance, not examined here, may have
261 differentially selected for the resilience abilities of natural populations worldwide. Finally, on
262 top of the side-effects of anthropisation, humans are known to actively select and facilitate
263 species around them that best fit their needs, potentially regardless of resilience properties.

264 Our work highlights the importance of studying short-term metrics in disturbance
265 ecology and ecology at large. Our resilience framework uses short-term (*i.e.*, transient)
266 demographic metrics[43,53–55] that we here show are rather responsive to human disturbances.
267 These metrics are, currently, not frequently used in demography[43], despite the fact that evidence
268 exists that short-term dynamics account for at least 50% of demographic variability in natural
269 populations, compared to other, more frequently used, long-term metrics[56]. Nonetheless, the
270 usage of these transient metrics is not free of risks. Indeed, the transient dynamic, and hence
271 our resilience metrics, are estimated from components of stage-structured population models
272 such as eigenvectors and eigenvalues, and these ultimately are shaped by the population's vital
273 rates[43,55]. Thus, these metrics speak to the inherent *potential* for resilience of a population. The

realised resilience is naturally best examined through experimental manipulations of disturbance regimes, an area of ecology that is currently lacking at the macro-ecological level, with notable exceptions such as DRAGNet, NutNet, and PlantPopNet.

Human pressure effects on vital rates and life history traits were for the most part indistinguishable in our study. Though the few traits significantly affected by human activities strengthened our hypothesis of a modulation of the demographic properties of species by human activities via underlying demographic processes, these occurred primarily through the ability of plants to shrink, and animals to accelerate their age at maturity near human settlements. Indeed, shrinkage increases the chances of survival either through saving on respiratory demands[46] and/or because it allows population to persist in disturbed and unsuitable environments waiting for better conditions to start growing again[47]. Shorter times to reproduction can also enable populations to adapt better to changing environments as it permits in certain conditions a higher number of mutants that can be adapted to this disturbed environments [57,58]. Moreover, and despite the lack of evidence of outcomes of human activities on reproductive rates in our study, other studies showing the effect of urbanization on the reproductive success and thereby demography of birds[59–61] does exist. This fact enlightens the need of combining both macroecological studies such as the present work, with long term monitoring and experiment-based research projects to better reflect and understand the ecological and evolutionary responses of species to disturbances.

We used model's residuals to control both for spatial and phylogenetic autocorrelation. To assess the reliability of our method, we ran separated phylogenetically and spatially controlled regression and compared the results of the different methods. Indeed, using residuals in further analyses to correct for the body mass or other parameters that bias the model is an common method in ecology[62]. However, this method does have certain limitations[63,64]; namely, it can provides biased estimates and it can increase the sensitivity of the significancy of

variables. Our results, using both residuals regression and separated regressions, showed similar results (see Supplementary Online Materials, Table S7-12). Hence, our method appears robust and reliable. Developing models that incorporate multiple corrections still remains a key challenge in macroecology[65]. Moreover, despite the value of the data contained in COMPADRE and COMADRE databases, geographic and taxonomic biases exist in them[66] (Figure S1), which could have affected our global description of the human correlates of population resilience. For instance, the representativeness of our sample size is rather low, with 279 species of plants representing *circa* 0.1% of all extant plants, and 45 species of animals <0.003% within kingdom Animalia.

Future steps should include the role of density dependence in population resilience in an explicit manner. Here, density dependence is only implicitly considered due to the lack of global demographic data with explicit estimates of density effects. Specifically, in our study, each of the carefully selected stage-structured population models are long-term means over the period of sampling in each peer-reviewed published study, where the population have likely been internally regulated through intra-specific competition. Tucker et al.[67] recently showed a link between mammal population density and human footprint index. Extending their hypothesis to a greater range of classes and studying the link between life history traits, human pressure, and population density will likely provide a better understanding of the situation and of the mechanisms that underpin these relationships and their relationship to population resilience. Similarly, including differential climate effects on species demography across the broad range of ecoregions we have examined here will be a valuable step forward, particularly since both plants and mammals from the same databases we use here have recently been reported to respond strongly climate extremes [68,69].

The correlates of human activities with different dimensions of population resilience show a different directionality between plants and animals, and even between animals

depending in their ability for long-distance mobility/migration. Indeed, the outcomes of human activities vary with the state of the environment and the populations. But, still, the significance of an effect of human pressure, especially human presence, on the resilience of species is confirmed in our analyses. Finally, we found a strong biotic homogenisation of the resilience strategies along an axis of human presence. This can be linked to multiple factors but remains an important concern for conservation policies.

Material and Methods

Resilience framework

To understand how human presence shape the resilience strategies of species, we examined the volume occupied by our populations in a space defined by their resistance, speed of recovery, compensation, and human pressure. We used the method described in Diaz et al. [70]. Briefly, this approach consist on quantifying convex hulls based on the empirical distribution of the resistance, recovery time, and compensation of our populations, compared to null model where these traits are (1) uniformly distributed between the maximum and the minimum values of the observations, (2) normally distributed with the mean and the variance of the normal distribution being equal to respectively the mean and the variance of the observations, (3) gamma distributed along the axis of human presence. To model the gamma distribution, we used the following parameters:

$$\begin{cases} k = \dfrac{\bar{x}^2}{S^2} \\ \theta = \dfrac{S^2}{\bar{x}} \end{cases}$$

with k being the shape and ϑ the scale of the gamma distribution, $\bar{x}$ the mean of the observed data and S^2 the variance of the observed data.

346

347 *Data provenance and selection*

348 To quantify human pressure, we used the Human Footprint (HFP)[40]. Importantly,
349 because the HFP is composed of eight layers that cover all terrestrial surface of the globe,
350 excluding Antarctic, at a 1km² resolution, this resource allows us to determine at a high spatial
351 resolution not only the overall effects of humans on the demographic resilience and life history
352 traits of natural populations, but also their underlying putative causes) (e.g., density of built
353 infrastructures, proximity to railways). The HFP assigns score of 50 based on multiple human
354 activities on the environment at each pixel. These layers of activity include human population
355 density, roads, navigable waterways, railways, night-time lights, built environment which is the
356 density of buildings and paved land estimated through satellites images analyses, pasture lands,
357 croplands (Fig. 1). Two sets of maps are available in the HFP, for 1993 and 2009. These two
358 years allow for a more comprehensive fit between the demographic data used here (below) and
359 the human pressure at the time of the record. Specifically, we matched the HFP scores of each
360 layer where demographic data was available to the year that was closest to when the
361 demographic data were collected.

362 To assign each of our studied natural populations a score of human-pressure, while
363 recognising the heterogeneity and potentially different effects of human activities, we used
364 multivariate analyses. We first performed a principal component analysis (PCA) on all eight
365 HFP layers. To do so, we rescaled the HFP map at a 10×10 km^2 resolution, sub-sampling just
366 one pixel in each grid cell. Next, we extracted 60,000 random data points from the 10 km² map
367 and used that subset of data to run the PCA analysis. Because the HFP data were linked to the
368 1993 or the 2009 HFP version, we ran a sensitivity analysis of the PCA outputs to compare the
369 results coming only from the 1993 map, from the 2009 map or from a mix of both. As the results

370 were quite similar (not shown), we took a subset of 60,000 random but unique points distributed
371 around the map and the two HFP dates.

372 To obtain data on species demography, we used the COMPADRE Plant Matrix
373 Database v.5.0.0[38] and the COMADRE Animal Matrix Database v.3.0.0[39]. These databases
374 contain 9,121 matrix population models (MPMs) of 760 plant species (Appendix 1), and 2,277
375 MPMs of 446 animal species, respectively (Appendix 1). MPMs are discrete-time structured
376 population models in which individuals are classified into discrete stages [71]. We then calculated
377 transient dynamics values that relate to key resilience quantities[43], vital rates[71], and life history
378 traits[32] for a mean MPM that summarises the dynamics of each of our 921 populations (See
379 supplementary material for more details about the demographic features obtention) (See
380 Appendix 2 for the list of demographic traits).

381 To check the robustness and validity of our comparative analyses, we assessed the
382 validity of our demographic data. We cleaned our dataset by removing suspect data and missing
383 values. We retained only terrestrial populations that had a full coverage of HFP data, a
384 population growth rate (λ) < 3 (we considered values above 3 as suspect for plant and animal
385 populations, as that would indicate too fast a growth for a natural population). We also removed
386 MPMs from populations that were subject to manipulations, and consequently MPMs that were
387 not estimated from natural conditions. Finally, we only kept the MPMs that were ergodic,
388 primitive, and irreducible to respect the Perron-Frobenius theorem requirements to calculate
389 growth-rate and some other matrix properties as well as to be sure that each MPM represented
390 a complete life cycle[72,73]. At the level of population projection, an ergodic matrix ensures the
391 user to obtain the same stable asymptotic growth rate regardless of initial population structure[54].
392 An irreducible matrix ensures that there will always be a pathway (direct or indirect) from one
393 stage or age class to another. Primitive matrices are ergodic, irreducible and aperiodic which
394 means that the greater common divisor of the life cycle lengths is 1 [74].

To reduce the number of traits to analyse, we removed those that were correlated. We examined the pairwise correlation between all the traits using the pearson correlation tests through the cor() function in R version 4.0.1[75]. To decide whether traits were correlated or not, we applied an arbitrary threshold value of 0.6. Therefore, when two traits had an absolute value of the coefficient of correlation superior to 0.6, they were considered correlated and we removed one of them, except in the case of the life-history traits that were all kept for future prospects.

Demographic traits regression

We developed two models to study the interaction between human activities through the PCA main dimensions and species' demographic resilience components. In both models, we controlled for trait variation due to the size of the individuals (*i.e.*, adult body mass for animals, maximum height for plants), spatial autocorrelation, the phylogenetic or evolutionary history autocorrelation, and the complexity of the life history that is estimated via the MPM dimension. Importantly here, it has been shown that life history traits scale with size in animals, especially in mammals[76,77]. Similarly, it has been shown that spatially close populations are more likely to be similar than distant populations than expected by pure chance[78,79].

To quantify and explicitly consider the effect of potential phylogenetic co-variation in traits in our analyses, we constructed two phylogenetic trees resolved down to the population level, one for plants (see Online Appendix), and another one for animals (see Online Appendix). We used Timetree[80] to create an animal phylogeny to accommodate our 109 populations from 45 examined animal species, and the package V.phylomaker[81] to create a plant phylogeny to accommodate our 796 populations from 279 examined plant species. As some sources in COMPADRE and COMPADRE contain multiple populations per species, we created our phylogenies at the population level instead of a species level. To do so, each population from

419 the same species was separated by a small distance (ε= 0.0000001 normalized units), thus
420 assuming that populations within a same species are very closely related. As the order of the
421 population divergences within our phylogenetic analyses might have an impact on the measure
422 of the phylogenetic signal and on the further correction, we ran sensitivity analysis of some
423 phylogenetic signals using different trees with a random order of the populations within the
424 tree. These sensitivity analyses showed no effect (not shown).

425 Our first model to test the effects of human pressure on demographic traits was based
426 on the study of the residuals after removing the effects of the confounding effects: animal
427 size/plant height, spatial autocorrelations, phylogenetic relationships. Technically, we
428 incorporated correction for body mass and plant height (later called size) in our study when
429 linearity was assessed in the relationship between the trait and the size. Next, we assessed the
430 effect of spatial autocorrelation on our models by calculating the Moran's index associated to
431 the different traits or to the residuals of the regression of the trait and size when a size effect
432 was detected. If spatial autocorrelation was found, we incorporated a correction for the location
433 in the model[82]. To do so, we used the tensor function of generalized additive models (gam) with
434 longitude and latitude [83,84] using R-package mgcv version 1.8-28. Finally, we ran a Markov
435 Chains Monte Carlo generalized linear mixed model (MCMCglmm) of the residuals of the traits
436 corrected (or not) for size and spatial autocorrelation on the HFP PCA main dimensions and
437 that consider the phylogeny of the populations.

438 Our second series of models to validate the new model developed are aimed to
439 disentangle spatial and phylogenetic corrections. As working on residuals can be a bit
440 controversial because one might neglect important pieces of information[63,64], we ran models
441 with similar parameters as previously described but without using residuals. In this case, we did
442 not correct for both spatial and phylogenetic autocorrelations together, but we ran the two
443 analyses separately. We included the size as an explicative parameter when it was relevant

(Fisher's exact test) and ran Markov Chains Monte Carlo generalized linear mixed model (MCMCglmm) to take evolutionary history into account and gam with longitude and latitude to take spatial distribution into account.

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Figure 1

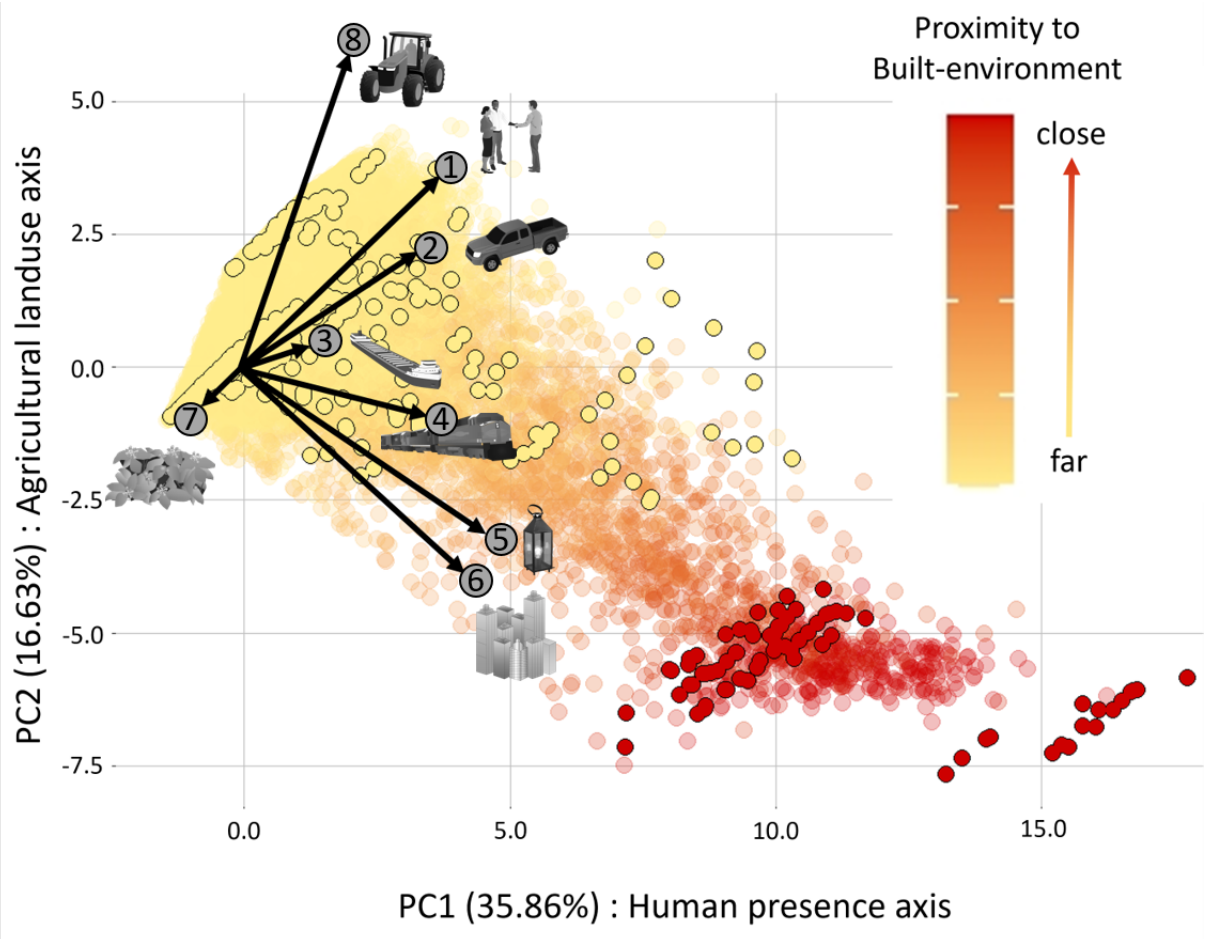


Figure 1. Principal Component Analysis (PCA) plot of terrestrial habitats worldwide, derived from the Human Footprint[40]. The PCA shows the two dominant axes of variation: PC1 corresponds to variation on human presence, and it is positively correlated with (1) human population density, (2) roads, (3) navigable waterways, (4) railways, and (5) light pollutions, (6) built environment, and it explains 35.86% of variation. PC2 differentiates locations according to land use, and it represents a trade-off between (7) extensive pastures, and (8) intense croplands, and it explains 16.63% of variation. Each dot corresponds to a terrestrial unit of 10 km^2 and is colour-coded according to its distance to a human-built environment, here defined as human produced areas that provide the setting for human activity (delimited using satellite imagery)[40]. Dots with a black circle correspond to our examined 921 natural

639 populations, showing the extensive coverage of our examined sites across pristine and human-
640 transformed habitats.
641

Figure 2

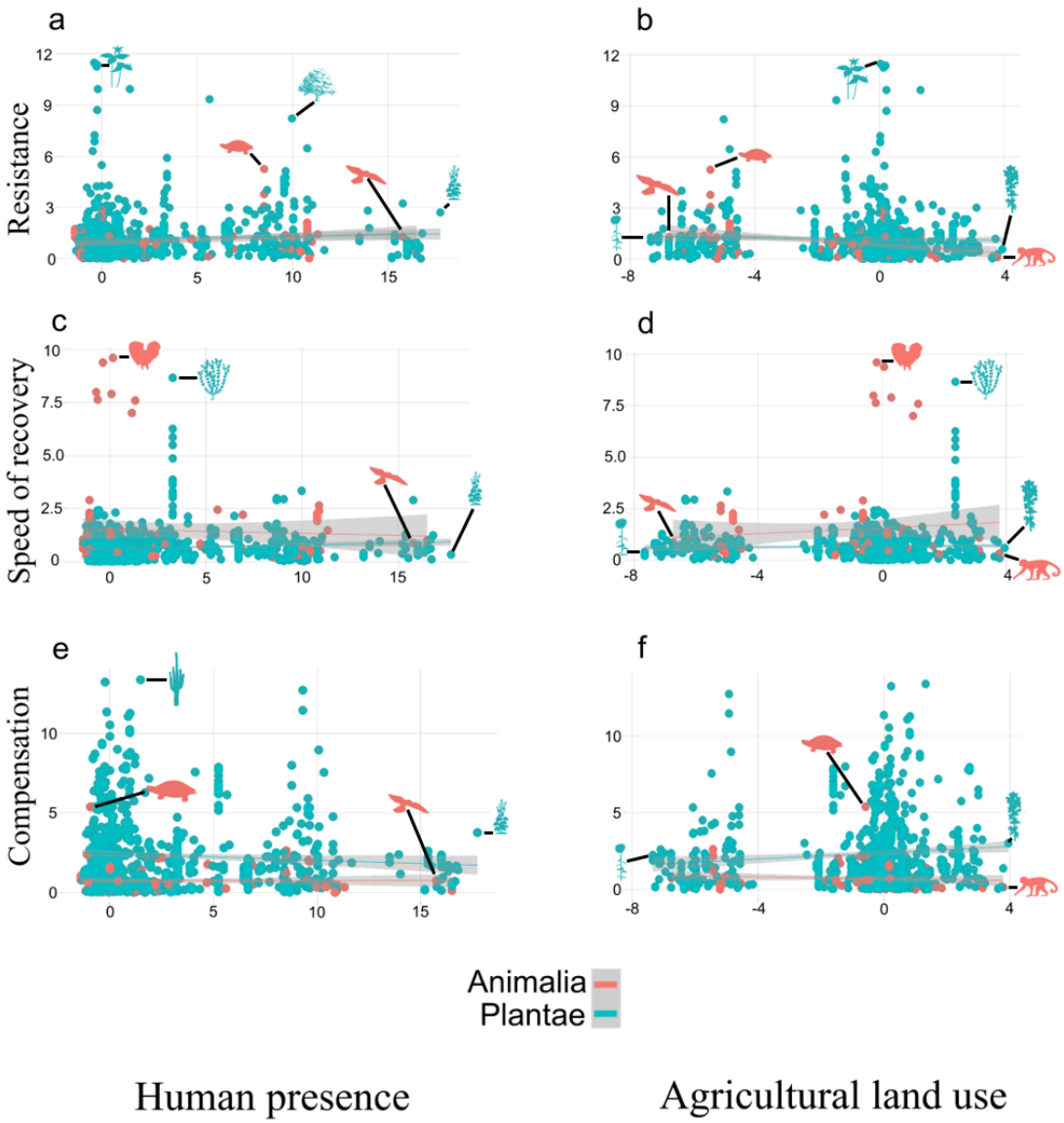


Figure 2. The examined components of demographic resilience correlate differently with human pressures on plants and animals. Correlation of three demographic resilience components (resistance, speed of recovery, and compensation) of our studied 921 natural populations along the continua of human presence (a, c, e) and agricultural land use (b, d, f) (See Figure 1). The shown linear fit describes the general correlations (orange: animals; green: plants), with the grey area representing 95% confidence intervals. A selected number of species are represented by silhouettes, from left to right: (a) *Trillium persistens* (persistent trillium),

Emydura macquarii (Macquarie turtle), *Cornus florida* (flowering dogwood), *Falco naumanni* (lesser kestrel), *Alliaria petiolata* (garlic mustard); (b) *Echinacea angustifolia* (narrow-leaved purple coneflower)*, Falco naumanni, Emydura macquarii, Trillium persistens, Dracocephalum austriacum* (Austrian dragon's head)*, Cebus capucinus* (Colombian white-face capuchin); (c) *Bonasa umbellus* (ruffed grouse), *Arenaria serpyllifolia* (thyme-leaf sandwort), *Falco naumanni*, *Alliaria petiolata*; (d) *Echinacea angustifolia, Falco naumanni, Bonasa umbellus, Arenaria serpyllifolia*, *Dracocephalum austriacum, Cebus capucinus*; (e) *Podocnemis expansa* (Arrau turtle), *Pseudomitrocereus fulviceps, Falco naumanni* ; (f) *Echinacea angustifolia, Podocnemis expansa, Dracocephalum austriacum, Cebus capucinus.*

Figure 3

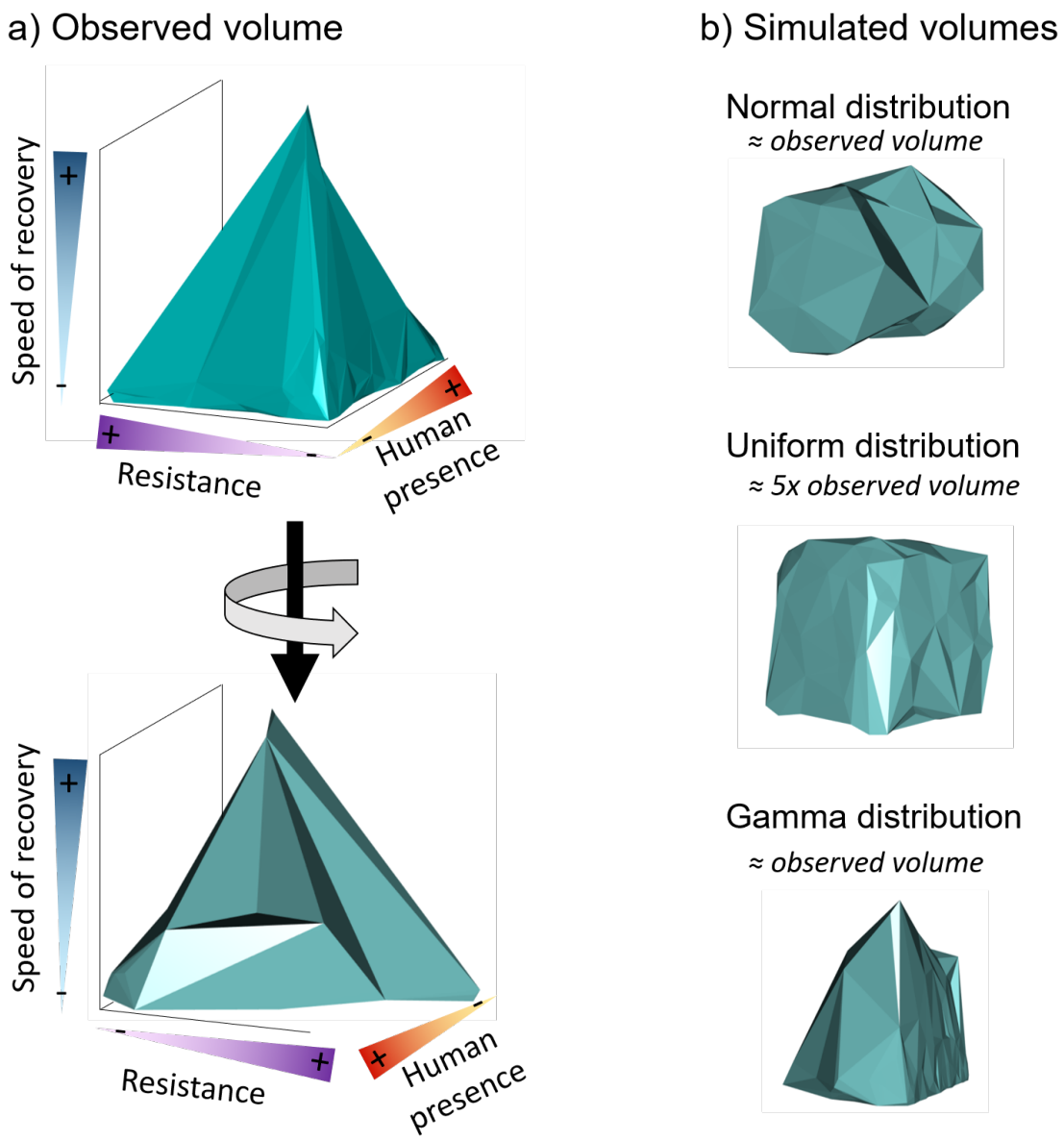
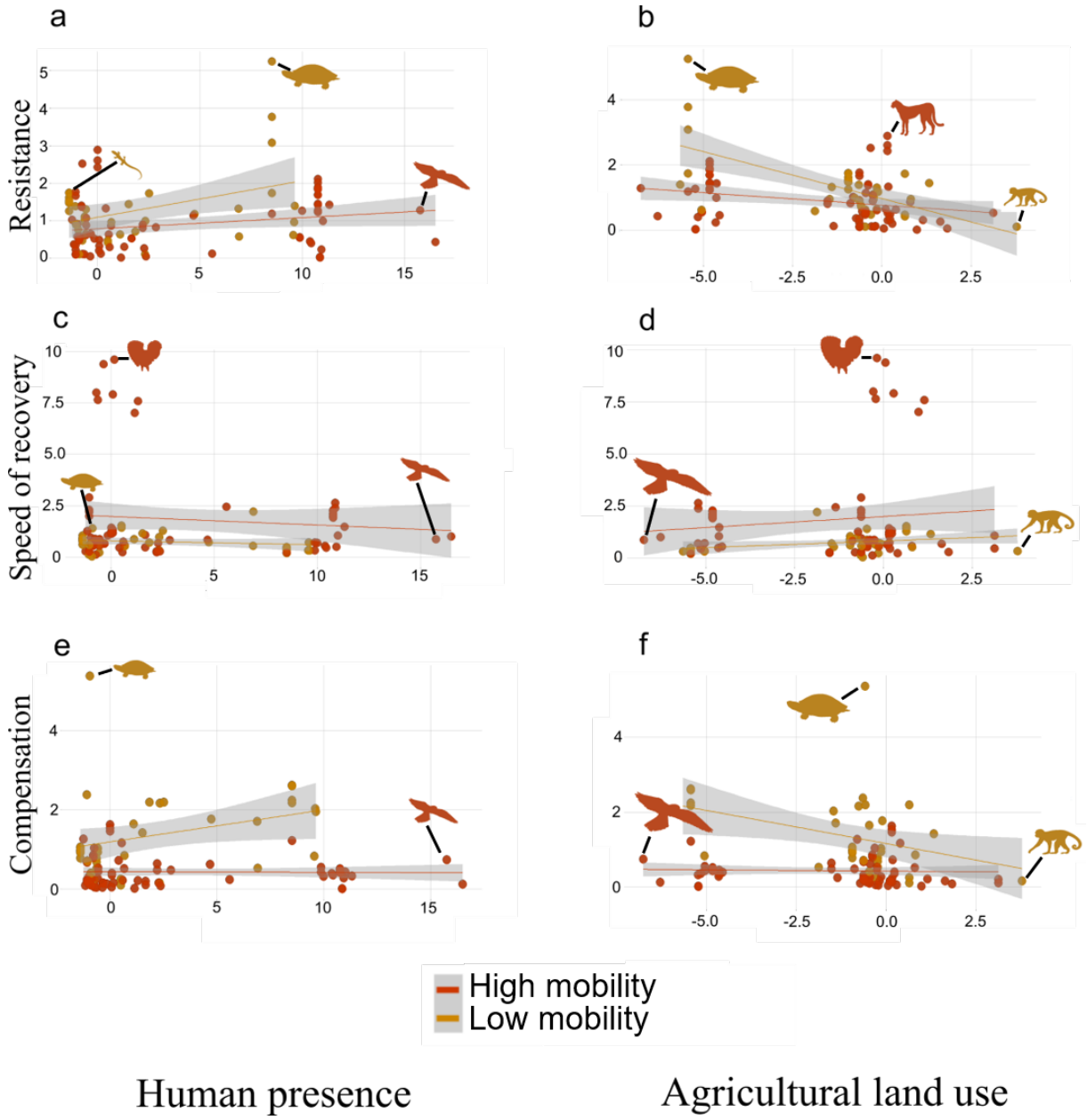


Figure 3. Human presence tightened the repertoire of resilience strategies. a) Plot of the 3D framework composed of human presence, recovery time and resistance (compensation is not displayed here for visual convenience). b) Comparisons of the volume of achieved strategies in the space defined by compensation – resistance –recovery time – human presence under the hypothesis of a normal distribution of the resistance and speed of recovery, a uniform distribution of the three same traits and the observed distributions in our populations (for graphical reason only 3D framework without compensation are displayed).

670 **Figure 4**



671

672 **Figure 4**. Low mobility species' demographic resilience is more strongly affected by human
673 pressures than high mobility species. Correlation of three key demographic resilience
674 components (resistance, speed of recovery, and compensation) of our studied 109 natural
675 populations along the continua of human presence (a, c, e) and agricultural land use (b, d, f)
676 (See Figure 1). The shown linear fit describes the correlations (brown: high mobility migration
677 [>100 km]; yellow: low mobility), with the grey area representing 95% confidence intervals. A

selected number of species are represented by silhouettes, from left to right: (a) *Sceloporus arenicolus* (dune sagebrush lizard)*, Emydura macquarii, Falco naumanni*; (b) *Emydura macquarii,, Acinonyx jubatus* (cheetah)*, Cebus capucinus*; (c) *Podocnemis expansa, Bonasa umbellus*, *Falco naumanni*; (d) *Falco naumanni, Bonasa umbellus, Cebus capucinus*; (e) *Podocnemis expansa, Falco naumanni* f) *Falco naumanni, Podocnemis expansa, Cebus capucinus.*

685 **Table 1**

Residual method for plants and animals				
Trait	Human presence axis	Agricultural land-use	Size correction	Spatial correction
a) Vital rates				
Survival	0.00 (0.03) -0.01 (0.25)	0.00 (0.89) -0.03 (0.15)	NO YES	YES NO
Growth	0.00 (0.72) 0.00 (0.64)	0.00 (0.66) 0.01 (0.61)	YES YES	YES YES
Shrinkage	0.01 (0.33) -	0.01 (0.78) -	YES -	YES -
Sexual reproduction	-0.04 (0.14) -0.00 (0.65)	0.04 (0.30) 0.00 (0.98)	YES YES	YES NO
Clonal reproduction	-0.01 (0.31) -	-0.02 (0.21) -	NO -	YES -
Shrinkage of pre-reproductive stages	0.01 (0.01) -	0.01 (0.06) -	NO -	YES -
Survival of reproductive stages	0.00 (0.86) 0.00 (0.60)	0.00 (0.81) -0.01 (0.73)	NO YES	YES YES
Growth of reproductive stages	0.01 (0.20) 0.00 (0.70)	0.01 (0.09) -0.03 (0.29)	YES YES	YES YES
b) Life history traits				
Net reproductive rate	0.03 (0.36) 0.06 (0.25)	0.04 (0.48) 0.13 (0.23)	YES NO	YES NO
Degree of iteroparity	-0.04 (0.30) 0.00 (0.96)	-0.05 (0.40) 0.01 (0.95)	NO YES	YES NO
Generation time	0.00 (0.94) 0.28 (0.08)	-0.01 (0.65) 0.51 (0.17)	YES YES	YES NO
Age at first reproduction	-0.02 (0.13) 0.01 (0.69)	-0.01 (0.72) -0.02 (0.81)	YES YES	YES YES
Rate of actuarial senescence	0.00 (0.49) -0.01 (0.37)	0.01 (0.29) -0.01 (0.81)	YES YES	YES NO
Probability of achieving maturity before dying	0.01 (0.17) 0.00 (0.88)	0.00 (0.72) 0.02 (0.42)	YES NO	YES YES

686

687 **Table 1**. The effects of human pressure are restricted to only a few demographic traits.

688 Summary of the results of the trait analysis for plants (light blue) and animals (light red) using

689 the residual method (i.e., the spatially and phylogenetically explicit method) described in
690 Methods. The human presence axis and agricultural land-use axis refer to the two main
691 dimensions of human activities from the Human Footprint database[40], as detailed in Figure 1.
692 The columns "size correction" and "spatial correction" indicate whether we applied such
693 corrections in the model (See Materials and Methods for further details on model choice). Note
694 that none of the examined animal populations include shrinkage or clonal reproduction (thus "-
695 "). P_{MCMC}-values parentheses with underline: $P_{MCMC}<0.05$; bold: $P_{MCMC}<0.001$.

696