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 developed 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

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

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

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The exponential growth that has characterised human societies since the industrial revolution has fundamentally modified our surroundings¹⁻⁵. Examples include rapid increases in agricultural fields, now accounting for 37% of the land surface⁶. Similarly, urban areas are projected to triple by 2030⁷. Recently, 59% of the Earth's terrestrial surface has been estimated to be under direct, negative impacts by human land use⁸. 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 Himalaya¹³, both by 2010. Ultimately, these fast reductions in species ranges affect the broad macroecological dynamics that regulate life on Earth¹⁴. 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 mammals¹⁹, birds²⁰, and plants²¹.

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 range²²⁻²⁴. 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 cycle²⁷), and that these strategies in turn determine the viability of natural populations²⁸.

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 strategies²⁹, the Competition-Stress Tolerator-Ruderal (CSR)³⁰, the fast-slow continuum³¹, and the parity continuum³². 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 species³². 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 COMPADRE³⁸ and COMADRE³⁹ databases, coupled with high-resolution human impact information via the Human Footprint database⁴⁰. 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 a 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 Footprint⁴⁰ 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,

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

To quantify the resilience of the 921 natural populations of our 324 examined species, we adopted a novel framework that classifies populations' inherent abilities to respond to disturbances using transient (*i.e.*, short-term) dynamics⁴². According to this framework, a population's intrinsic resilience can be quantified as per its resistance, speed of recovery, and compensation to shocks (*i.e.* sudden increase in population size after a disturbance)⁴³. Next, we predicted these three dimensions of demographic resilience using the two principal component axes of human activities described above via (i) a spatially and phylogenetically explicit model, and also (ii) linear models. The former models allowed us to explicitly consider spatial and phylogenetic autocorrelations, while also estimating the role of phylogenetic inertia in our observed patterns. Our proxy to phylogenetic inertia, Pagel's λ ⁴⁴, was relatively high with the resistance metrics both for plant ($\lambda = 0.958$, $P < 0.001$) and animals ($\lambda = 0.936$, $P < 0.001$). It was also high for the two other components of demographic resilience (see Table S4).

The demographic resilience of plant and animal populations differ in their association with human activities. Our analyses reveal that animal populations tend to be more resistant (t -test_{df=107} = 2.357, $P = 0.020$) (Fig. 2a; Table S5) than plants when found closer to humans (t -test_{df=788} = 1.508, $P = 0.132$). On the contrary, animal populations exhibit a lower resistance in intense agricultural areas (t_{107} = -3.872, $P < 0.001$), while plant population resistance is not affected by agricultural land use. The speed of recovery to disturbances in plant populations located near human presence is greater than in pristine habitats (t_{788} = 2.976, $P = 0.003$). While the speed of recovery of animal populations is faster than plants ($t_{112.46}$ = 4.35, $P < 0.001$), this demographic resilience component is independent of proximity to human presence for animals. Interestingly, according to phylogenetically informed models, resistance decreases for plant 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 hulls⁴⁵. 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 $\approx$ simulated volume, $P <$

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

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

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

Human pressure effects of species demographic resilience are modulated via their impacts on only a limited set of vital rates and life history traits. To test hypothesis H3, that human pressures will correlate with changes in underlying vital rates and life history strategies, we developed a spatially and phylogenetically explicit model that accounts for adult body mass (for animals) or maximum height (for plants), separately (See Methods and Supplementary Online Materials). Surprisingly, the vital rates structuring our populations are not significantly affected by the effects of human presence, agricultural land use, nor their interaction (Table 1a). A notable exception is the ability of plants to shrink from one year to the next, which is positively correlated with both axes of human activities. In our pool of plant species, individuals in populations closer to human-transformed habitats tend to shrink more than those in pristine habitats. This finding is in agreement with studies that have shown that plant shrinkage increases chances of survival⁴⁶, likely through the cut down in respiratory demands⁴⁷, and a recent work showing that plant populations persist in unsuitable environments thanks to their ability to shrink²⁴. Indeed, plant populations closer to human presence have slightly higher survival rates than in pristine habitats. Similarly, life history traits linked to reproduction are not affected by human pressures (Table 1b). Most life history traits do not respond to human pressures, except for generation time in animals, which tends towards a slight increase closer to human settlements (Table 1b). Further analyses, where animal species are separated based

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

Discussion

Using a novel framework that quantifies and compares components of demographic resilience across vastly different species⁴³, we show how human presence and human activities have shaped –and especially constrained– the repertoire of demographic resilience strategies across 921 populations from 326 animal and plant species worldwide. Our findings also highlight how species that lack the ability for long-distance mobility/migration are more deeply impacted by human activities. The employed demographic resilience framework illustrates how human pressure affects a key aspect of demography: a populations ability to resist, recover, and even, in some cases, grow after a disturbance. Our convex hulls show a clear thinning of the resilience hypervolume of natural populations in urban habitats compared to pristine ecosystems. Closer to human settlements and intense agricultural areas, we report species with greater degrees of resistance and recovery time, but a narrow range of resilience. This finding in highly anthropised areas supports the hypothesis of abiotic homogenisation of resilience traits with intense human pressures^{48,49}. Together, our findings suggest that human activities have filtered out less resilience species.

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

human environments characterized by intense, frequent disturbances. An alternative explanation for this pattern is that low-resilience species might not have been present in areas where humans have settled and transformed the land. Indeed, humans have mostly settled in places with a high primary production and relatively stable climates⁵⁰. However, these locations, by offering conditions that are not too extreme and relatively stable hence, should have selected for species with adaptations to disturbances. Indeed, resilience strategies to disturbances often come at a cost to organisms, which thus can be too expensive to persist in environments where they are not that frequently used⁵¹. Consequently, maintaining some resistance aspect would be done at the expense of some other functions, leading to a reduced competitive ability in stable environments⁵². Furthermore, here we have worked only under the prism of the outcomes of human activities and infrastructures. It is possible that key social aspects of human societies as well as natural disturbance, not examined here, may have differentially selected for the resilience abilities of natural populations worldwide. Finally, on top of the side-effects of anthropisation, humans are known to actively select and facilitate species around them that best fit their needs, potentially regardless of resilience properties.

Our work highlights the importance of studying short-term metrics in disturbance ecology and ecology at large. Our resilience framework uses short-term (*i.e.*, transient) demographic metrics^{43,53–55} that we here show are rather responsive to human disturbances. These metrics are, currently, not frequently used in demography⁴³, despite the fact that evidence exists that short-term dynamics account for at least 50% of demographic variability in natural populations, compared to other, more frequently used, long-term metrics⁵⁶. Nonetheless, the usage of these transient metrics is not free of risks. Indeed, the transient dynamic, and hence our resilience metrics, are estimated from components of stage-structured population models such as eigenvectors and eigenvalues, and these ultimately are shaped by the population's vital 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 demands⁴⁶ and/or because it allows population to persist in disturbed and unsuitable environments waiting for better conditions to start growing again⁴⁷. 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 birds⁵⁹⁻⁶¹ 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 ecology⁶². However, this method does have certain limitations^{63,64}; namely, it can provides biased estimates and it can increase the sensitivity of the significance 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 macroecology⁶⁵. Moreover, despite the value of the data contained in COMPADRE and COMADRE databases, geographic and taxonomic biases exist in them⁶⁶ (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:

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

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.

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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 km² 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

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

To obtain data on species demography, we used the COMPADRE Plant Matrix Database v.5.0.0³⁸ and the COMADRE Animal Matrix Database v.3.0.0³⁹. These databases contain 9,121 matrix population models (MPMs) of 760 plant species (Appendix 1), and 2,277 MPMs of 446 animal species, respectively (Appendix 1). MPMs are discrete-time structured population models in which individuals are classified into discrete stages⁷¹. We then calculated transient dynamics values that relate to key resilience quantities⁴³, vital rates⁷¹, and life history traits³² for a mean MPM that summarises the dynamics of each of our 921 populations (See supplementary material for more details about the demographic features obtention) (See Appendix 2 for the list of demographic traits).

To check the robustness and validity of our comparative analyses, we assessed the validity of our demographic data. We cleaned our dataset by removing suspect data and missing values. We retained only terrestrial populations that had a full coverage of HFP data, a population growth rate (λ) < 3 (we considered values above 3 as suspect for plant and animal populations, as that would indicate too fast a growth for a natural population). We also removed MPMs from populations that were subject to manipulations, and consequently MPMs that were not estimated from natural conditions. Finally, we only kept the MPMs that were ergodic, primitive, and irreducible to respect the Perron-Frobenius theorem requirements to calculate growth-rate and some other matrix properties as well as to be sure that each MPM represented a complete life cycle^{72,73}. At the level of population projection, an ergodic matrix ensures the user to obtain the same stable asymptotic growth rate regardless of initial population structure⁵⁴. An irreducible matrix ensures that there will always be a pathway (direct or indirect) from one stage or age class to another. Primitive matrices are ergodic, irreducible and aperiodic which means that the greater common divisor of the life cycle lengths is 1⁷⁴.

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 4.0.1⁷⁵. 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 Timetree⁸⁰ to create an animal phylogeny to accommodate our 109 populations from 45 examined animal species, and the package V.phylomaker⁸¹ 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

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

Our first model to test the effects of human pressure on demographic traits was based on the study of the residuals after removing the effects of the confounding effects: animal size/plant height, spatial autocorrelations, phylogenetic relationships. Technically, we incorporated correction for body mass and plant height (later called size) in our study when linearity was assessed in the relationship between the trait and the size. Next, we assessed the effect of spatial autocorrelation on our models by calculating the Moran's index associated to the different traits or to the residuals of the regression of the trait and size when a size effect was detected. If spatial autocorrelation was found, we incorporated a correction for the location in the model⁸². To do so, we used the tensor function of generalized additive models (gam) with longitude and latitude^{83,84} using R-package mgcv version 1.8-28. Finally, we ran a Markov Chains Monte Carlo generalized linear mixed model (MCMCglmm) of the residuals of the traits corrected (or not) for size and spatial autocorrelation on the HFP PCA main dimensions and that consider the phylogeny of the populations.

Our second series of models to validate the new model developed are aimed to disentangle spatial and phylogenetic corrections. As working on residuals can be a bit controversial because one might neglect important pieces of information^{63,64}, we ran models with similar parameters as previously described but without using residuals. In this case, we did not correct for both spatial and phylogenetic autocorrelations together, but we ran the two 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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Literature

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Figure 1

Figure 1. Principal Component Analysis (PCA) plot of terrestrial habitats worldwide, derived from the Human Footprint⁴⁰. 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 km² 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),

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

660

661 **Figure 3**

662

663 **Figure 3.** Human presence tightened the repertoire of resilience strategies. a) Plot of the 3D

664 framework composed of human presence, recovery time and resistance (compensation is not

665 displayed here for visual convenience). b) Comparisons of the volume of achieved strategies

666 in the space defined by compensation – resistance –recovery time – human presence under the

667 hypothesis of a normal distribution of the resistance and speed of recovery, a uniform

668 distribution of the three same traits and the observed distributions in our populations (for

669 graphical reason only 3D framework without compensation are displayed).

670 **Figure 4**

671 Human presence Agricultural land use

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

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

684

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

the residual method (i.e., the spatially and phylogenetically explicit method) described in Methods. The human presence axis and agricultural land-use axis refer to the two main dimensions of human activities from the Human Footprint database⁴⁰, as detailed in Figure 1. The columns “size correction” and “spatial correction” indicate whether we applied such corrections in the model (See Materials and Methods for further details on model choice). Note that none of the examined animal populations include shrinkage or clonal reproduction (thus “-”). P_{MCMC} -values parentheses with underline: $P_{MCMC} < 0.05$; bold: $P_{MCMC} < 0.001$.