

Cumulative and interactive effects of global change drivers on population and biodiversity change

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Description

Please give a brief description of your study, including some background, the purpose of the study, or broad research questions.

Background

All across the globe, species' populations and the biodiversity of ecological communities are changing in complex ways^{1–5}. Against a backdrop of accelerating global change, a critical research challenge is to disentangle the sources of the heterogeneous patterns of population and biodiversity change. Despite multiple calls for more comprehensive tests of the effects of global change drivers on ecological changes^{6,7}, our current knowledge has largely been limited by a focus on individual types of environmental change, such as forest loss^{8–10} and warming¹¹. As a result, we know very little about how multiple types of anthropogenic activities are jointly influencing the ongoing restructuring of ecological communities^{6,7,12} and whether their effects are amplified when acting together^{6,13,14}. Ecosystems are usually simultaneously exposed to a suite of global change drivers, such as climate change, human use, population density, pollution and invasion pressure (Figure 1). A key research step is to test the synergy and discord between the effects of multiple types of environmental change on populations and biodiversity (Figure 2). Interactions between global change drivers could arise through multiple mechanisms. Land-use change, specifically forest clearing, can lead to a loss of cooler microhabitats across the landscape¹⁵, thus making cold-tolerant species more vulnerable to climate warming^{16–21}. Rising temperatures can facilitate habitat restoration by lifting physiological constraints on tree seedling growth across latitudes, thus accelerating secondary succession²². Warming and alterations in precipitation regimes have also been linked with both increases and decreases in species' vulnerability to land-use change²³. Recent compilations of long-term population²⁴ and biodiversity time-series²⁵, together with global maps of the intensities of climate change, human use, population density, pollution and invasion pressure²⁶, allow us to quantitatively test the cumulative and interactive effects of global change drivers on ecological change across taxa and study ids (Figure 1). Unravelling how interactions between multiple global change drivers are reshaping Earth's biota can provide key, but currently missing, evidence for international policies and predictions of ecological changes across the Anthropocene^{6,7,27}.

Purpose of the study

Our aim is to quantify how global change drivers influence individual species and entire ecological communities over time (Figures 1, 2 and 5). Specifically, we will focus on the effects of climate change, human use, human population density, pollution and invasion pressure on temporal changes in population abundance, species richness and community composition

(turnover), as these drivers capture the variety of ways in which humans are altering the planet²⁶. We will test if the individual, cumulative and interactive effects of the different types of global change explain the heterogeneous patterns of population and biodiversity change observed across the planet.

Research questions

1. How do global change drivers, including climate change, human use, population density, pollution and invasion pressure influence population and biodiversity change?
2. What are the cumulative effects of global change drivers on population and biodiversity change?
3. Are there interactive effects of human use and climate change on population and biodiversity change?

CUMULATIVE AND INTERACTIVE EFFECTS OF GLOBAL CHANGE ON POPULATIONS AND BIODIVERSITY

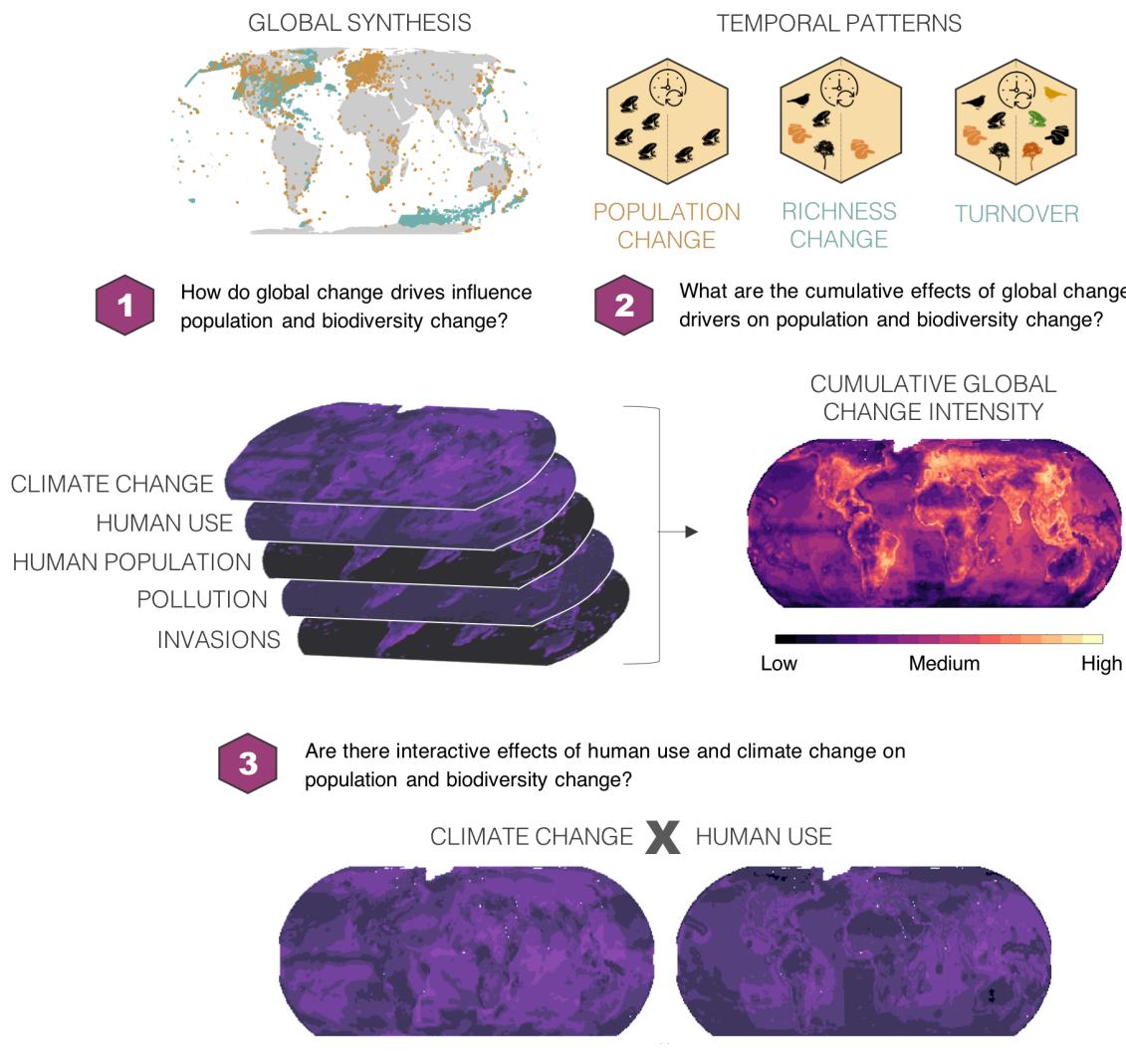


Figure 1. Our synthesis quantitatively tests the effects of global change on population and biodiversity change across the Anthropocene. The diagram shows the main concept and research questions of our study.

Hypotheses

List specific, concise, and testable hypotheses. Please state if the hypotheses are directional or non-directional. If directional, state the direction. A predicted effect is also appropriate here. If a specific interaction or moderation is important to your research, you can list that as a separate hypothesis.

In our hypotheses and throughout the pre-registration, we refer to different types of ecological change and how they are influenced by global change. The key terms we use, as well as the relationships between them, are outlined in Figure 2.

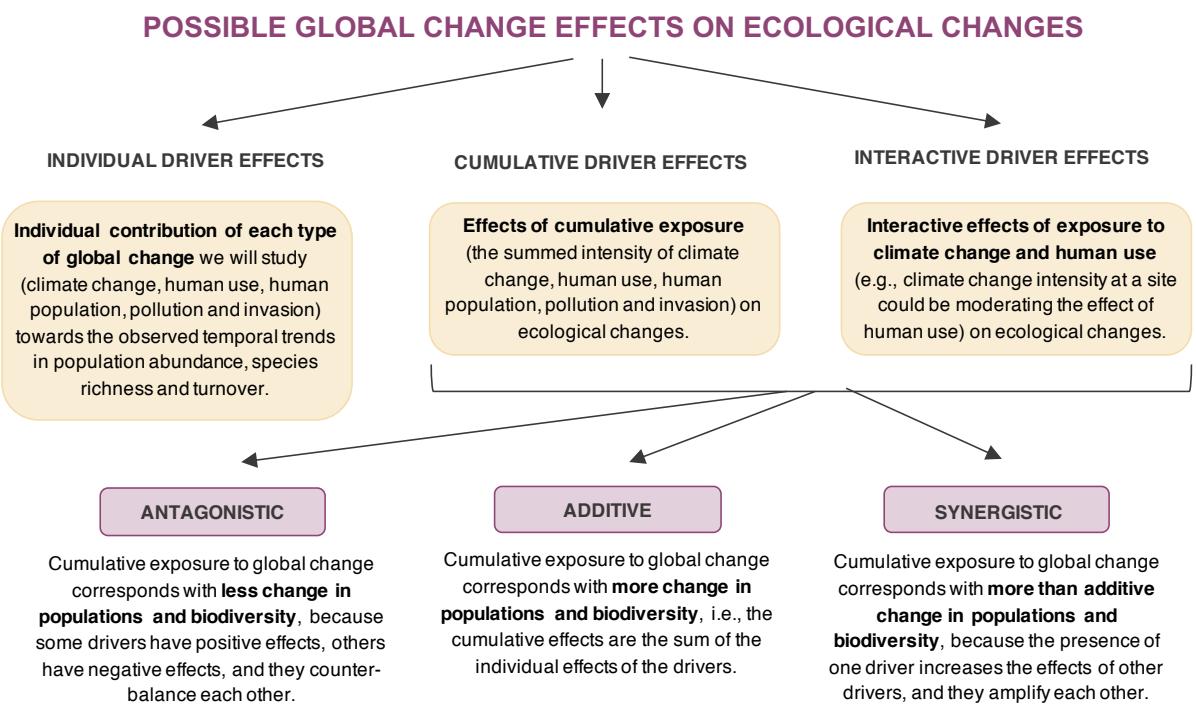
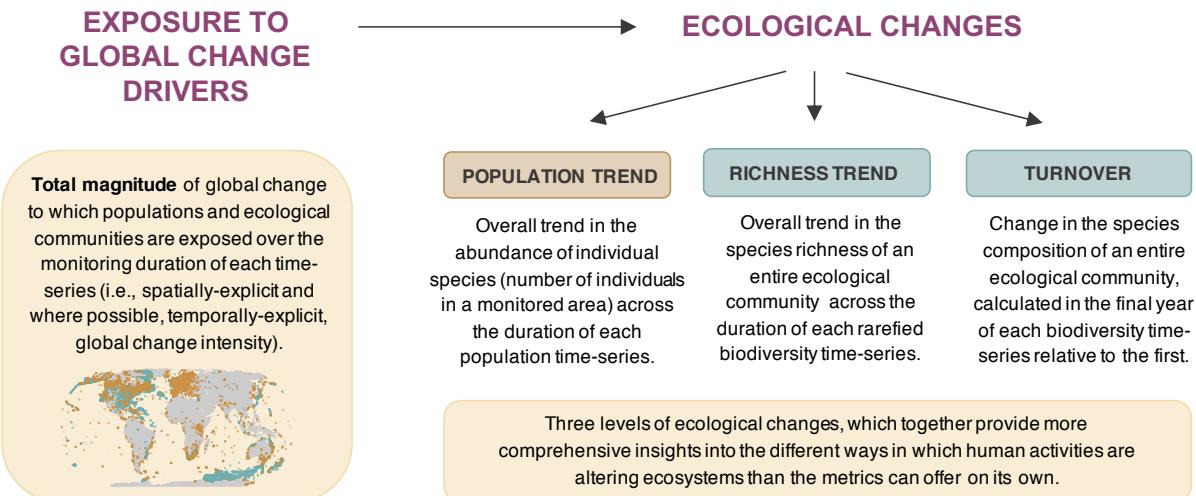


Figure 2. Exposure to global change drivers alters ecosystems in a variety of ways, and the possible cumulative and interactive effects of multiple types of drivers can be antagonistic, additive or synergistic.

1. How do global change drivers influence population and biodiversity change?

Hypotheses

- Larger exposure to climate change corresponds with greater increases in population abundance and species richness at temperate and polar latitudes, and with greater declines in population abundance and species richness at tropical latitudes.
- Larger exposure to human use and pollution and denser human population correspond with greater declines in population abundance and species richness across all latitudes.
- Larger exposure to invasion pressure corresponds with greater declines in population abundance across all latitudes.
- Larger exposure to invasion pressure corresponds with greater increases in species richness across all latitudes.
- Larger exposure to each type of global change corresponds with greater species turnover within ecological communities across all latitudes.

We predict greater population increases in temperate and polar areas that are experiencing higher intensities of climate change, because warming, the aspect of climate change that is better understood, reduces physiological constraints on the fitness of most species, thus increasing survival and the number of individuals within a population^{28–31} (but see Spooner et al. 2018¹¹ for negative effects of warming for mammals and birds). We predict greater declines in population abundance and species richness with greater exposure to climate change at tropical latitudes because for species living closer to their warmer thermal limit, warming can increase physiological constraints^{30,32}. Ongoing analyses from our team have found that temperature warming is associated with increases in species richness³³. Such a pattern can arise from the poleward movement of species tracking their climatic optima, corresponding with local colonisations by new species³⁴, which exceed the rate of local extinctions, but this overall positive richness effect can vary with latitude, with increases in temperate and polar areas and decreases in tropical areas³⁵ (Figure 4).

We predict greater declines in population abundance and species richness with greater exposure to human use activities, denser human population and higher pollution due to niche constraints and fitness reductions caused by this suite of anthropogenic threats^{9,36–39}. We expect greater declines in population abundance with higher exposure to invasions because species' invasion can limit the resources available for native species^{40,41}. Conversely, we predict increases in species richness with higher exposure to invasions because the establishment of new species is often quicker than the potential local extinction of the original species⁴².

We predict larger turnover with larger exposure to all types of global change because the different drivers all alter ecosystems, which might create beneficial conditions for some species, and detrimental conditions for others, resulting in community composition changes^{43,44}.

2. What are the cumulative effects of global change drivers on population and biodiversity change?

Hypotheses

- Exposure to multiple drivers leads to antagonistic effects on population and species richness change.
- Exposure to multiple drivers lead to synergistic effects of global change drivers on community composition change (turnover).
- Effect sizes of both these types of effects become larger with increasing cumulative driver intensity across both the marine and the terrestrial realm.
- The spatial heterogeneity in population and biodiversity change is explained by distinct combinations of global change drivers acting at similar intensities in different areas of the world (e.g., coastal regions on different continents are exposed to similar types and amounts of global change).

Predictions

Species can be affected in different ways by environmental change, often predicted to be mediated by their intrinsic traits (e.g., habitat and temperature preferences^{28,45}). The set of traits that make a species sensitive to one driver may make the same species also sensitive to other drivers⁴⁶. Alternatively, species sensitive to one driver may be less sensitive to other drivers⁴⁷. In the latter case, cumulative exposure to different drivers may have counterbalancing effects with opposing directions, resulting in non-directional trends in species richness and population abundance^{48–52}. Antagonistic effects of multiple global change drives would align with the heterogeneous, but centered on zero, trends in population abundance¹ and species richness^{2,3} over time at sites around the world. Thus, we predict a greater prevalence of antagonistic effects of global change drivers on population and species richness change over time at sites around the world (Figure 3).

As global change drivers increasingly alter ecosystems^{26,53,54}, the resulting environmental change facilitates colonisations by new species^{55,56}, but also leads to local extinctions and changes in relative abundance^{43,57}. When multiple drivers are present and species vary in their vulnerability to threats⁴⁷, larger proportions of the community might be affected compared to when only one driver is in place⁵⁸, leading to an accelerated reshuffling of ecological communities. Thus, we predict synergistic effects of global change drivers on community composition, with turnover increasing with greater exposure to human exploitation, climate change, pollution and invasion pressure.

Finally, we predict that species' exposure to distinct combinations of global change drivers²⁶ explains the signatures of local-scale population¹ and biodiversity change² over time, because when the same combinations of drivers occur in different areas, they might be reshaping ecosystems, and thus the species and communities they support, in similar ways.

- *If we find declines and/or no directional changes in population and biodiversity trends with higher cumulative exposure to multiple global change drivers, we infer antagonistic*

effects on population size, species richness and community composition, meaning that global change drivers act in opposing directions.

- If we find linear increases in population and biodiversity change with higher cumulative exposure to multiple global change drivers, we infer additive effects on population sizes, species richness and community composition, i.e., the drivers act in the same direction, but do not amplify each other's effects.
- If we find non-linear population and biodiversity change with higher simultaneous exposure to multiple global change drivers, we infer synergistic effects, i.e. the drivers act in the same direction and amplify each other's effects.
- If we find distinct signatures of the different driver combinations in the patterns of population and biodiversity change around the world, this will mean that species' exposure is a key predictor of responses to global change drivers that overrides or is positively correlated with the effects of local environmental factors and species' vulnerability.
- Alternatively, no driver combination signatures in the patterns of population and biodiversity change will suggest that local environmental factors, species' vulnerability to threats and their traits are mediating responses to global change drivers, creating complex fine-scale patterns that are not captured by larger scale categorical classifications of global change.
- The current version of the driver combination categories²⁶ characterised spatial pattern of drivers that have accumulated over a long time period, e.g. the amount of urban cover is one element of human use-driven global change and urbanisation has been occurring for centuries. Thus, the driver categorisation might also fail to explain variation in recent population and biodiversity change if recent patterns of anthropogenic change are spatially distinct from the long-term patterns of anthropogenic change and there are time lags in population and biodiversity responses⁴⁴.

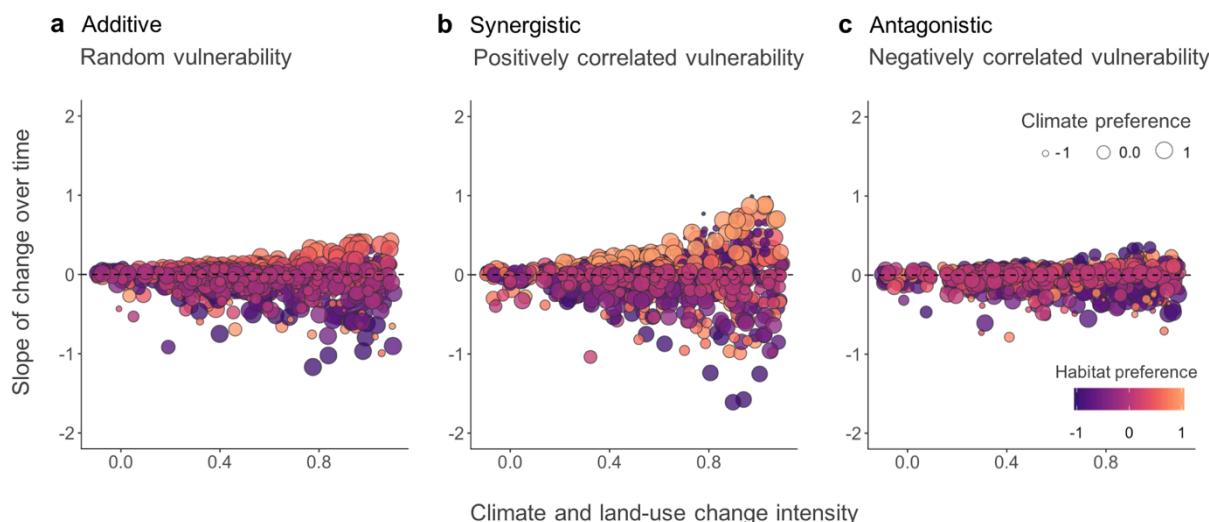


Figure 3. Patterns of cumulative effects of climate and land-use change on change over

time (in this case population abundance, where each point is the slope for one population over time) under different scenarios of species' vulnerability. Graphs show outputs of simulation models, where each site experienced different amounts of climate and land-use change and species responses were regulated based on their climate and habitat preferences. When species vulnerability to the two drivers is correlated, we find more change over time, whereas if a species responds positively to land-use change, but negatively to climate change, we find less change in population abundance over time.

3. Are there interactive effects of human use and climate change on population and biodiversity change?

Hypotheses

- The magnitude of population and richness change declines as exposure to both human use activities and climate change increases (negative interactive term, antagonism).
- The magnitude of turnover increases as exposure to both human use activities and climate change increases (positive interactive term, synergy).

Prediction

We predict smaller population and richness changes with higher simultaneous exposure to human use activities and climate change because of antagonistic interactions between the two drivers^{6,22,23}. Such antagonistic interactions can arise due to human use activities having in general negative effects on population abundance and species richness and climate change, specifically warming, usually correlating with increases in abundance and richness, especially in temperate and polar regions^{9,28,33} (Figure 4).

We predict greater turnover with increasing intensity of climate- and human use-related drivers, especially in the subtropical and temperate latitudes of the planet where new species are invading following poleward range shifts^{23,33,59}, potentially replacing some of the resident species, and the original species pool is further reshuffled due to intensive agriculture and exploitation of natural resources^{8,9,56} (Figure 4).

We expect that the interactive effects of climate change and human use on population and biodiversity trends over time will be mediated by latitude across both the marine and terrestrial realms, because of known gradients in how climate change and human use intensity and biodiversity are distributed across the planet. The global distribution of biodiversity has a peak concentrated in the tropics, climate change intensity increases towards the poles, but human use decreases in the same direction. We predict that these gradients will influence the magnitude and direction of the ways in which global change drivers together reshape populations and biodiversity (Figure 4).

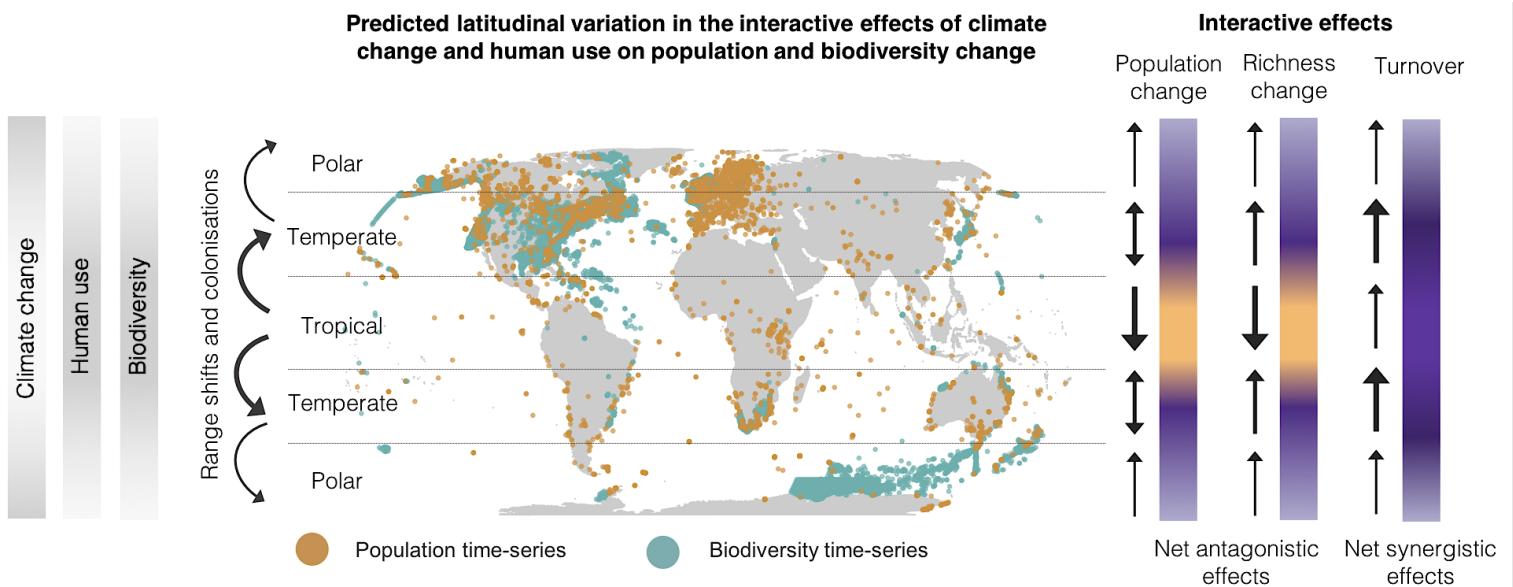


Figure 4. We predict that the interactive effects of climate change and human use on population change, richness change and turnover will vary across latitudinal bands due to known latitudinal gradients in climate change, human use and biodiversity. Arrows show direction and magnitude (arrow width).

- If we find greater turnover with increasing intensities of both climate and human use-related drivers, this will mean that the two types of drivers correspond with local extinctions and colonisations of different types of species and are acting in synergy, thus affecting larger proportions of ecological communities⁵⁸. Such patterns suggest that species' vulnerability to different global change drivers is negatively correlated⁴⁷, in line with evolutionary trade-off theory⁶⁰.
- Conversely, a lack of increase in turnover with greater intensities of both climate and human use-related drivers will suggest that the two types of drivers influence ecological communities in different ways and are having antagonistic effects when acting together. If one driver has led to the local extinction of a species, a second driver cannot cause the local extinction of the same species again⁵⁸, and some species show positive correlation in their vulnerability to different types of threats^{23,61,62}, as predicted by Brown's niche breadth hypothesis⁶³.

Study design

Describe your study design. Examples include two-group, factorial, randomized block, and repeated measures. Is it a between (unpaired), within-subject (paired), or mixed design?

Describe any counterbalancing required. Typical study designs for observation studies include cohort, cross sectional, and case-control studies.

Our study will test the relationships between temporal changes in populations and biodiversity and 1) the individual intensities of global change drivers, 2) their cumulative intensities, and 3)

the interaction between climate change and human use (Figure 1). Our analyses will encompass the marine and terrestrial realms and will be based on observation studies of population abundance, species richness and community composition over time. We will not include observations from manipulated experiments. Our work will be based on a data synthesis integrating population and biodiversity trends from 46,467 locations around the world (Figure 5). These locations represent repeated surveys of species abundance and biodiversity (the identity and abundance of all species found within an ecological assemblage). The time-series duration varies, with a minimum of at least five survey points. The sites were surveyed independently of one another, i.e., we do not have paired control-impact studies.

Both the Living Planet and the BioTIME databases under-represent less studied taxa, such as invertebrates and amphibians (Figure 5). The Living Planet Database does not capture sites that have experienced the extreme end of human use intensity (Figure 7). The BioTIME database underrepresents locations that have experienced the extremes of the climate change spectrum, especially in the terrestrial realm, which might influence the climate change effects we detect on species richness change and turnover (Figure 7). Nevertheless, the locations capture variation in the intensity of global change on the planet (Figures 6 and 7). We will not exclude any sites based on driver intensity (i.e. we will not focus only on places with high driver intensity) and will study how the full continuous range of global change influences populations and biodiversity. Using global maps of some of the main global change drivers²⁶, we will extract mean driver intensity over ~96km² polygons around the locations of each population and biodiversity time-series. The biodiversity data have already been rarefied to account for variation in sampling effort and study area size in Blowes and Supp *et al.* 2018², where there are more methodological details. The driver data have been harmonised to a common resolution (100km² cells) to enable comparison among the effects of different types of anthropogenic pressure. The resolution at which we will calculate driver intensity is larger than the roaming ranges of small-bodied animals and less mobile species. Because of the magnitude of different species and communities that we will be analysing, it is not possible to have an analytical scale tailored to the traits of each species and community. Furthermore, it is still largely unknown what is the optimal scale at which to conduct macroecological studies, and finer resolution global driver data are not currently available for most drivers. For more details on analytical methods, see the statistics section further down.

Explanation of existing data

If you indicate that you will be using some data that already exist in this study, please describe the steps you have taken to assure that you are unaware of any patterns or summary statistics in the data. This may include an explanation of how access to the data has been limited, who has observed the data, or how you have avoided observing any analysis of the specific data you will use in your study.

Our study is fully based on existing data and we will not execute any first-hand data collection. However, our study will be the first to integrate these specific datasets of population time-series, biodiversity time-series and global change intensity. Population and biodiversity data

are freely available in the Living Planet and BioTIME Databases (see references for details on data collection)^{24,25}. The Living Planet Database can be accessed on http://www.livingplanetindex.org/data_portal. The BioTIME Database can be accessed on Zenodo (<https://doi.org/10.5281/zenodo.1211105>) or through the BioTIME website (<http://biotime.st-andrews.ac.uk/>). The global change driver data represent the output of Bowler *et al.* 2018⁴⁹, where they are described in detail. The driver data we will use are spatially-explicit, but current data limitations prevent us from extracting temporally-explicit intensity values for all drivers. For details on the individual layers forming the global change data we will use, including their resolutions and temporal coverage, see Table S1 in Bowler *et al.* 2018²⁶.

We are aware of the patterns in population change¹, biodiversity change², global change drivers²⁶, the effects of forest cover change on population and biodiversity trends⁸ and the effects of temperature warming on abundance and species richness trends³³, which all represent previous analyses members of our team have led. The present study is the natural next step of the previous work of our team. No member of the authorship team for this study has explored patterns or summary statistics of the cumulative and interactive effects of global change on population and biodiversity trends using the specific datasets we will use. All team members either already have access to the data, or can be granted access upon request, but analyses will begin only after the pre-registration is complete. The characteristics of the population and biodiversity data we will use are visualised in Figure 5, and the global change intensities our study sites represent are visualised in Figure 6. The structure of the data (12 sample data rows) is presented in the *sample_data.csv* file. Each variable is described in the measured variables section further down.

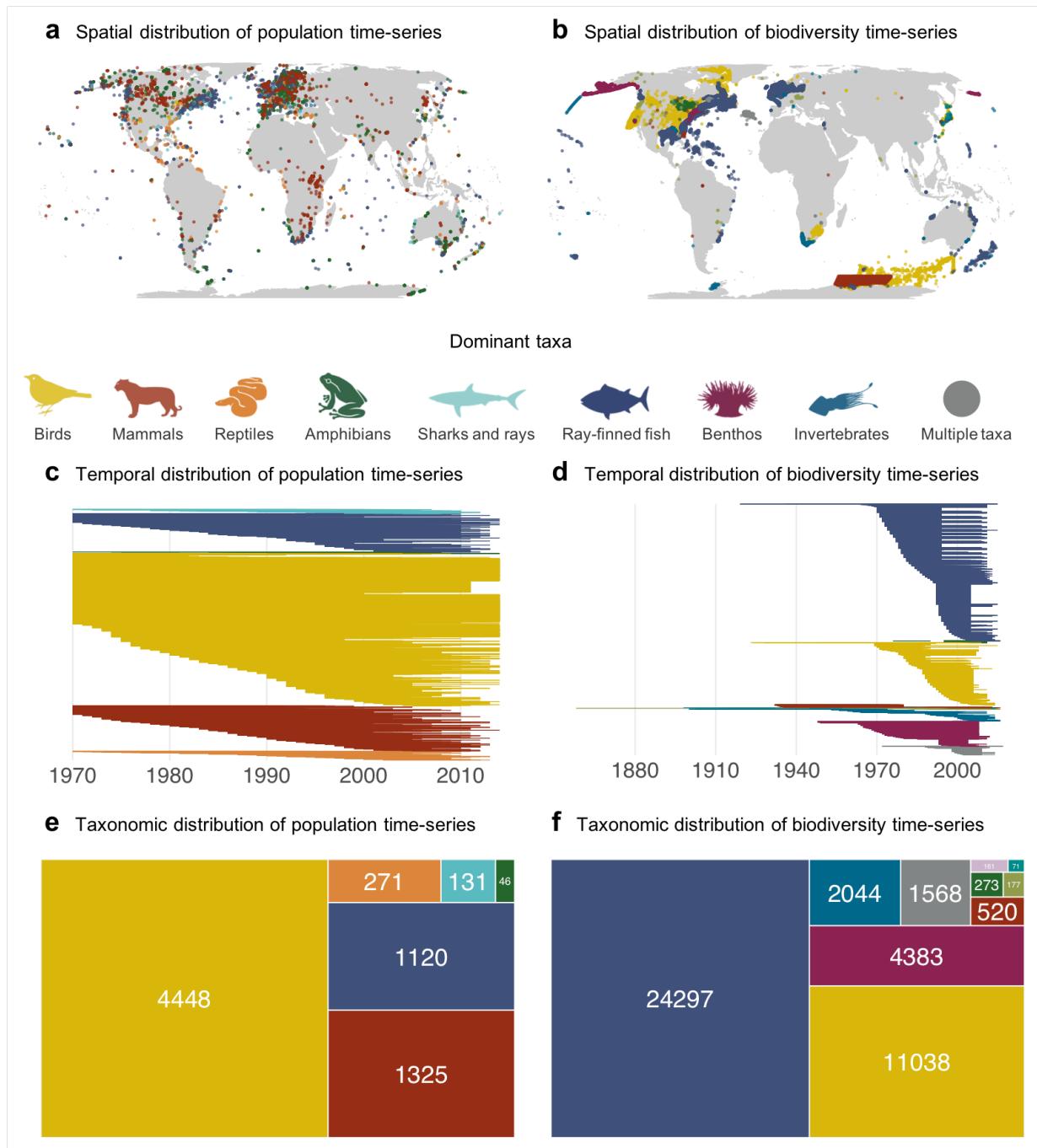


Figure 5. Our study synthesises population and biodiversity time-series data across space, time and taxa. Note that the time scales on **c** and **d** are different to allow the visualisation of variation in the population time-series.

Data collection procedures

Please describe the process by which you will collect your data. If you are using human subjects, this should include the population from which you obtain subjects, recruitment efforts, payment for participation, how subjects will be selected for eligibility from the initial pool (e.g.

inclusion and exclusion rules), and your study timeline. For studies that don't include human subjects, include information about how you will collect samples, duration of data gathering efforts, source or location of samples, or batch numbers you will use.

Our study integrates several already available global databases and thus we did not execute any first-hand data collection and instead integrated existing datasets. For data integration procedures, see the attached R script. The data integration did not involve blinding, as no experiments or field data collection were undertaken, and our aim was to include the most representative sample of temporal vertebrate population records possible. We did not execute randomization. We will work with all available population and biodiversity time-series that meet our data inclusion criteria (see sample size rationale). We will work with observational data and we will categorise time-series based on the taxa of organisms they included and the study id in which the specific time-series were located.

Sample size

Describe the sample size of your study. How many units will be analyzed in the study? This could be the number of people, birds, classrooms, plots, interactions, or countries included. If the units are not individuals, then describe the size requirements for each unit. If you are using a clustered or multilevel design, how many units are you collecting at each level of the analysis?

The total sample size for our study represents 51,871 records of trends in population abundance, species richness and community composition (turnover) as well as the intensities of global change drivers at each site. The current sample size breakdown for each category within our data is outlined in Table 1. Both the BioTIME and Living Planet databases are living databases that are continuously augmented as more data become available and thus, before we begin our analysis, we will revisit the databases and if new data have been added, our sample size will increase relative to Table 1. We will explore the possibility of using the BioTIME database for population-level analyses, in addition to the community-level ones (species richness and turnover). Because the BioTIME database contains records of both the number of species and their abundance, it is possible to quantify the trends of each species' population over time. Adding population-level trends from BioTIME will mean that we increase our sample size for the population analyses, making our tests more comprehensive and covering a larger variety of species. However, there are possible methodological issues that might prevent us from using the population-level BioTIME data, such as difficulties in distinguishing if individuals from different plots in the same study are part of the same population. For the spatial, temporal and taxonomic representation of the current data, see Figure 5.

Table 1. Sample sizes for all categories within our data.

Type	Realm	Taxa	Time-series
Population	Terrestrial	Amphibians	46
		Birds	3447
		Mammals	1036

		Reptiles	111
	Marine	Ray-finned fish	1120
		Birds	1001
		Sharks and rays	131
		Mammals	289
		Reptiles	160
Biodiversity	Terrestrial	Terrestrial plants	177
		Birds	1600
		Mammals	40
		Terrestrial invertebrates	71
		Multiple taxa	30
		Amphibians	273
	Marine	Birds	9438
		Fish	24297
		Mammals	480
		Marine invertebrates	2044
		Benthos	4383
		Multiple taxa	1538
		Marine invertebrates/plants	161

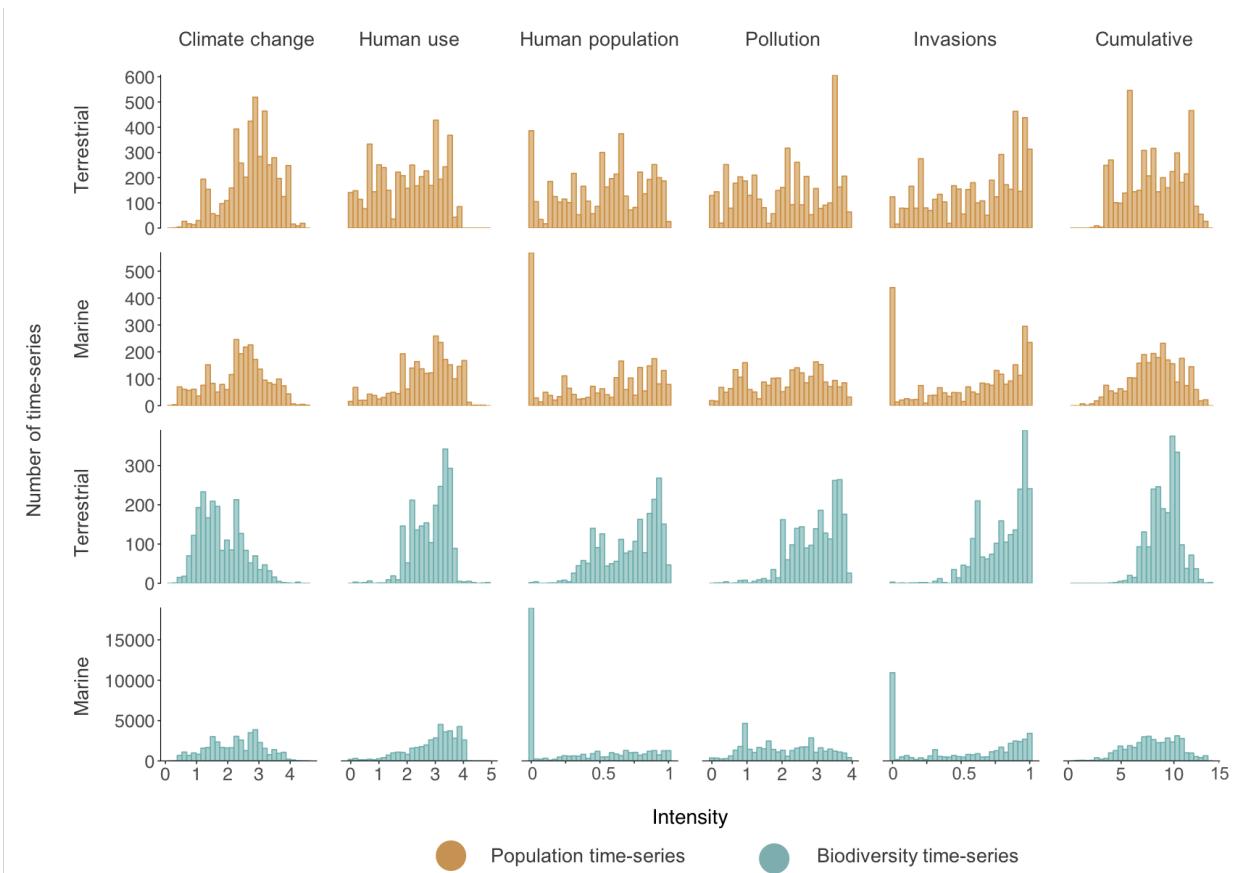


Figure 6. The intensity of global change varies across the sites represented in our analysis. Histograms show the number of time-series categorised by each level of driver intensity. Note that zero inflation in human population and invasion intensity for marine population and biodiversity time-series is because they are from remote locations with no inhabitants (i.e., in one of the world's oceans) and far from trade routes (proxy for invasion pressure).

Sample size rationale

This could include a power analysis or an arbitrary constraint such as time, money, or personnel.

The spatial scale of our analyses is terrestrial and marine ecosystems globally. Thus, we did not predetermine sample size and instead worked with all available temporal population and biodiversity data that met our criteria – the time-series are located within the terrestrial or marine realm, the time-series includes at least five survey points in time (thus making the minimum time-series duration five years), and the time-series is from a taxon with at least 40 time-series in total included in the analyses.

Stopping rule

We will be working with all available population and biodiversity time-series from the terrestrial and marine realms, coming from the Living Planet and BioTIME Databases. Both databases are continuously augmented. We want to provide as comprehensive of an examination of global change effects on populations and biodiversity as possible. In the event of new additions to the databases while we are conducting our analyses, we will check if they match our inclusion criteria (at least five survey points, located in the terrestrial or marine realm and enough taxonomic representation within the existing data). For example, currently there are 12 terrestrial reptile biodiversity time-series in BioTIME and because that falls short of our guideline of around at least 40 time-series per taxa, we have excluded those data. However, if there are 28 new reptile time-series added to BioTIME before we submit our manuscript, we will redo our analyses using the latest data.

Measured variables

Describe each variable that you will measure. This will include outcome measures, as well as any predictors or covariates that you will measure. You do not need to include any variables that you plan on collecting if they are not going to be included in the confirmatory analyses of this study.

Response variables:

Population trend – the overall trend in population abundance across the duration of each time-series. The population time-series represent repeated monitoring surveys of the number of individuals in a given area (species' abundance over time), hereafter called “populations”. This variable is the output of Daskalova *et al.* 2018¹.

Richness trend - the overall trend in species richness across the duration of each rarefied biodiversity time-series. This variable is calculated as in Daskalova *et al.* 2018⁸.

Turnover – the change in species composition due to species replacement, calculated in the final year of each time-series relative to the first. This variable is derived in Blowes and Supp *et al.* 2018².

Explanatory variables:

The mean intensity of climate change, human use, human population, pollution and invasion pressure for the ~96 km² grid cells within which the population and biodiversity records fall.

The cumulative intensity of the aforementioned drivers (continuous variable)

The driver combination at each site (categorical variable)

The interaction term between climate change and human use

The explanatory variables are the output of Bowler *et al.* 2018²⁶

Metadata:

Time-series id – an identification number for each time-series.

Realm – categorical variable (Terrestrial/Marine)

Study id – categorical variable, the study id within which each time-series is located, following the study ids defined in Olson and Dinerstein 2002⁶⁴.

Taxa – categorical variable, see Table 1 for all levels.

Species – categorical variable for population data only, the species which each population represents.

Latitude and longitude – the geographical coordinates of each time-series.

Duration – continuous variable, the duration of each time-series, varies across time-series, with a minimum value of five years.

Start and end year – the first and last year of monitoring for each time-series.

Examples of all variables can be found in the sample data csv file.

Indices

If any measurements are going to be combined into an index (or even a mean), what measures will you use and how will they be combined? Include either a formula or a precise description of your method. If you are using a more complicated statistical method to combine measures (e.g. a factor analysis), you can note that here but describe the exact method in the analysis plan section.

Our measures of global change driver intensity (climate change, human use, human population, pollution, invasion pressure and cumulative driver intensity) represent combined indices of multiple layers of input data capturing anthropogenic activities. For more details on the methods behind the global change input driver layers and how the global change metrics were calculated, see Bowler *et al.* 2018²⁶.

Our metric of cumulative driver intensity represents the sum of the values for each individual driver layer. Some of the intensities of the input driver layers are correlated, e.g. pollution and human population (Figures 6 and 7) and using both layers implicitly gives higher weight to this type of global change within our overall index of cumulative driver intensity⁶⁵. An alternative approach is to explicitly weight the different types of global change in the calculation of the cumulative intensity metric, as is done with the Human Footprint Index⁶⁶. However, explicit weighting relies on evidence of the importance of each driver for populations and biodiversity which is not available for the majority of the species we will study and thus, we will not use variance-weighting. A third alternative is to use an ordination analysis to reduce the dimensionality of the input driver data and base the cumulative driver intensity metric on the two axes that explain most of the variation in global change across our study sites. We will conduct sensitivity analyses to determine how the calculation of the cumulative driver intensity index varies based on these three methodologies.

Statistical models

What statistical model will you use to test each hypothesis? Please include the type of model (e.g. ANOVA, multiple regression, SEM, etc) and the specification of the model (this includes each variable that will be included as predictors, outcomes, or covariates). Please specify any interactions, subgroup analyses, pairwise or complex contrasts, or follow-up tests from omnibus tests. If you plan on using any positive controls, negative controls, or manipulation checks you may mention that here. Remember that any test not included here must be noted as an exploratory test in your final article.

We will use hierarchical models in a Bayesian framework through the R package *brms* v2.1.0⁶⁷ in R v3.5.1⁶⁸, which provides a Stan interface for R. We will model the marine and terrestrial data separately as we expect that the two realms will be influenced by global change in different ways²⁶. Our analysis is based on a two-stage modelling framework. In the first stage, we calculated population trends (Daskalova *et al.* 2018¹), richness trends and turnover (Daskalova *et al.* 2018⁸). In the present study, we will undertake the second stage of the analysis where we will model population and biodiversity trends across global change driver intensity. An alternative analytical framework would be to combine the two stages of the analyses into one integrated model, e.g., as in Bjorkman *et al.* 2018⁶⁹. However, for our study this is not possible because our population change estimates are derived from state-space models (see Daskalova *et al.* 2018¹ for details), while the biodiversity trends are derived using generalised linear models. These two different types of modelling frameworks cannot be streamlined into one combined model, but they both individually represent the optimal way to analyse the different type of data (population-level vs community-level data). The specific structure of each statistical model is outlined below, with the presented priors representing weakly informative priors. We will also explore the possibility of carrying through the uncertainty around population trends, richness trends and turnover into our second stage models by further restricting the priors to cover the distribution of error around the response variables.

Fixed effects

All models will include a duration fixed effect because our time-series are of varying lengths. Additionally, we will include a categorical latitudinal band fixed effect (tropical, temperate and polar), because of known latitudinal gradients in both biodiversity and global change intensity (Figure 4). The only set of models that will not include a latitudinal band fixed effect are the driver combination models in Question 2, because the aim of that question is to test the predictive power of a set of global change categories, irrespective of latitude. The remaining fixed effects are question specific and are outlined below.

Random effects

All models will include a study id random effect to account for the clustering per study (e.g., multiple time-series can come from the same study), as well as the spatial clustering of the data. The population change models will also include a species random effect to account for

the possible correlation between the trends of populations from the same species. The richness and turnover models are based on community-level data (multiple species in one assemblage) and thus in those models we will also include a taxa random effect because of the potential confounding effects of taxonomic group and study id. We will first run the models with both random intercepts and random slopes and if model convergence is not achieved, we will use models with only a random intercept. There are multiple studies per species in the population change data, and similarly, there are multiple studies per taxa in the biodiversity data, and to account for the structure of the data, we will use nested random effects structures (*species / study id* and *taxa / study id*, respectively).

1. How do global change drives influence population and biodiversity change?

For each of our response variables (population trend, richness trend, turnover), we will run a separate model where we test the effects of the individual global change drivers on their own.

*mu ~ climate change intensity * latitudinal band + duration, random = species / study id*
*mu ~ human use intensity * latitudinal band + duration, random = species / study id*
*mu ~ human population density * latitudinal band + duration, random = species / study id*
*mu ~ pollution intensity * latitudinal band + duration, random = species / study id*
*mu ~ invasion pressure intensity * latitudinal band + duration, random = species / study id,*

where *mu* represents the population trend of each population time-series as derived from state-space models (see Daskalova et al. 2018¹ for detailed methods on how population change was quantified). The population change models will assume a Gaussian error.

To test the effects of global change drivers on richness change, we will use the following models:

*richness trend ~ climate change intensity * latitudinal band + duration, random = taxa / study id*
*richness trend ~ human use intensity * latitudinal band + duration, random = taxa / study id*
*richness trend ~ human population density * latitudinal band + duration, random = taxa / study id*
*richness trend ~ pollution intensity * latitudinal band + duration, random = taxa / study id*
*richness trend ~ invasion pressure intensity * latitudinal band + duration, random = taxa / study id,*

where *richness trend* represents the trend in species richness of each biodiversity time-series over time as derived from generalized linear hierarchical models with a Poisson error (*richness ~ year*, see Daskalova et al. 2018⁸ for detailed methods on how richness change was quantified). The models of richness trend versus driver intensity will assume a Gaussian error.

For our final metric, turnover, the models will have structures as outlined below:

$turnover \sim climate\ change\ intensity * latitudinal\ band + duration, random = taxa / study\ id$
 $turnover \sim human\ use\ intensity * latitudinal\ band + duration, random = taxa / study\ id$
 $turnover \sim human\ population\ density * latitudinal\ band + duration, random = taxa / study\ id$
 $turnover \sim pollution\ intensity * latitudinal\ band + duration, random = taxa / study\ id$
 $turnover \sim invasion\ pressure\ intensity * latitudinal\ band + duration, random = taxa / study\ id,$

where *turnover* represents the changes in community composition due to species replacement, calculated in the final year of each biodiversity time-series relative to the first. The metric uses Jaccard's dissimilarity, where zero means that the community composition has stayed exactly the same and one represents a complete change in species. For detailed methods on how beta diversity was partitioned into turnover and nestedness, see Baselga 2010⁷⁰. The turnover models will be based on a zero one inflated beta distribution to account for the properties of turnover (bounded between zero and one, inclusive, where one is a complete change in species composition). The probability density function for the zero one inflated beta distribution is:

$$betainf(y; \alpha, \gamma, \mu, \phi) = \begin{cases} \alpha(1 - \gamma), & y = 0 \\ \alpha\gamma, & y = 1 \\ (1 - \alpha)\gamma f(y; \mu, \phi), & 0 < y < 1, \end{cases}$$

where α is the probability that a zero or one occurs, γ is the probability that a one occurs (given an observation is a zero or a one), and μ and ϕ are the mean and precision of the beta distribution, respectively. For $y = 0$ and $y = 1$, α and γ will be modelled assuming a Bernoulli distribution and logit-link function, and we will fit models with only an intercept. For $0 < y < 1$, we will assume a beta error distribution and a logit-link function.

The general properties of the models will remain the same for all research questions, thus below we outline the general prior specifications and model characteristics, noting that the distributions and priors we use will stay the same for the models for research questions two and three as well (e.g., turnover will always be modelled with a zero one inflated beta distribution).

For all models except those where the response variable is turnover (which will be a zero one inflated model), we will use weakly regularising normally-distributed priors for the global intercept and slope:

$$\beta_0 \sim gaussian(0, 6),$$

$$\beta_1 \sim gaussian(0, 6).$$

For the turnover models, we will use the following priors:

$$\beta_0 \sim gaussian(0, 6),$$

$$\beta_1 \sim gaussian(0, 6),$$

$$zoi \sim gaussian(0, 0.5),$$

$$coi \sim gaussian(0, 0.5),$$

where zoi is the probability of being a zero or a one and coi is the conditional probability of being a one (given an observation is a zero or a one).

Group-level parameters (the species random effect in the population change models, i , the taxa random effect in the richness and turnover models, j , and the study id random effect in all models, k) were all assumed to be $gaussian(0, \sigma)$, and priors on the σ were the same for all models:

$$\sigma_{\beta0j} = \sigma_{\beta0j, k} = \sigma_{\beta0j, k, i} \sim half\ Cauchy(0, 2).$$

We will initially run models for 6000 iterations, with a warm up of 2000 iterations, and three MCMC chains and will increase these metrics if chain convergence is not obtained. We will assess convergence visually by examining trace plots and using $Rhat$ values (the ratio of the effective sample size to the overall number of iterations, with values close to one indicating convergence).

2. What are the cumulative effects of global change drivers on population and biodiversity change?

Below we outline the model structures, for details on distributions and priors, see statistical descriptions for question one.

$mu \sim cumulative\ intensity\ of\ global\ change\ drivers * latitudinal\ band + duration,$

$random = species / study\ id$

$richness\ trend \sim cumulative\ intensity\ of\ global\ change\ drivers * latitudinal\ band + duration,$

$random = taxa / study\ id$

$turnover \sim cumulative\ intensity\ of\ global\ change\ drivers * latitudinal\ band + duration,$

$random = taxa / study\ id$

The cumulative driver intensity is a single continuous metric and for example, a value of 0.5 can be the result of a combination of different types of drivers around the world. Thus, we will also run models with a categorical variable, driver combination. The driver combination captures whether a time-series from a given location is exposed to e.g., climate change and pollution, or climate change and invasion pressure. Both combinations can result in the same cumulative driver magnitude, but the underlying drivers are different. Thus, the models below will allow us to test if there are distinct signatures of the different combinations of global

change drivers in population and biodiversity trends around the world. For details on the clustering analyses which produced the different driver combinations, see Bowler *et al.* 2018²⁶.

mu ~ driver combination + duration, random = species / study id
richness trend ~ driver combination + duration, random = taxa / study id
turnover ~ driver combination + duration, random = taxa / study id

3. Are there interactive effects of human use and climate change on population and biodiversity change?

Below we outline the model structures, see statistical descriptions for question one for details on distributions and priors. We will test for possible latitudinal effects in the relationships between population and biodiversity change and the interactive effects of global change drivers by adding a categorical latitudinal band fixed effect in our models (Figure 4). From the magnitude and direction of the interactive effect, we will be able to determine if when human use and climate change occur together, their influence on populations and biodiversity is dampened or intensified and how that varies across three latitudinal bands – tropical, temperate and polar.

*mu ~ human use * climate change * latitudinal band, random = species / study id*
*richness trend ~ human use * climate change * latitudinal band, random = taxa / study id*
*turnover ~ human use * climate change * latitudinal band, random = taxa / study id*

Additional analyses

Simulations

The temporal trends of species' abundance and the richness and composition of ecological communities are likely a product of the interaction between species' exposure to global change and species' traits – characteristics like habitat breadth, temperature tolerance, diet, etc. In the present study, we focus on the effects of exposure to multiple global change drivers. Our analyses include over 20,000 species and trait data are not available for all of them. Furthermore, the integration of time-series data with trait data poses significant challenges that represent a future research direction. Nevertheless, to explore the interaction between species' traits, exposure to global change, and population and biodiversity trends, we will conduct three simulations (one per metric – population change, richness change, turnover). We will simulate populations and ecological communities, as well as their habitat and temperature breadth. The populations and communities will be exposed to scenarios representing the possible combinations between randomly distributed traits in a community, positively correlated traits (e.g., the species vulnerable to human use are also vulnerable to climate change), negatively correlated traits (e.g., the species vulnerable to human use respond positively to climate change), randomly occurring climate change and use intensities, positively correlated climate change and human use intensities (e.g., a community experiencing climate change is also exposed to a similar amount of human use intensity), and negatively correlated climate change

and human use intensities. We will use the simulations to test the possible mechanisms by which the patterns we find using empirical evidence (see analyses described above) could arise. If we find no directional effects of cumulative or interactive effects of multiple global change drivers on population and biodiversity trends, this result will suggest high inter- and intra-specific trait variation that might be producing a wide variety of responses to global change. By simulating trait variance across populations and communities, the simulations will allow us to test the possible influence of traits on ecological changes across the Anthropocene.

Study reproducibility

We will make all R code used in our analyses publicly available at time of publication in a GitHub repository. We will also make code and data available to reviewers at time of manuscript submission. We will archive a library of all the specific versions of all used R packages. To enable full reproducibility, we will also make the model input and output data for all statistical analyses publicly available.

Transformations

If you plan on transforming, centering, recoding the data, or will require a coding scheme for categorical variables, please describe that process.

We will center all explanatory variables in our statistical models with a mean of zero. The driver intensity explanatory variables were already scaled to be between 0 and 1 to allow comparison between different types of drivers in Bowler et al. 2018²⁶. For visualisation purposes and to aid comparison, we will standardise the effect sizes from our models by dividing the posterior mean by the standard deviation of the input data for each model.

Inference criteria

What criteria will you use to make inferences? Please describe the information you'll use (e.g. specify the p-values, Bayes factors, specific model fit indices), as well as cut-off criterion, where appropriate. Will you be using one or two tailed tests for each of your analyses? If you are comparing multiple conditions or testing multiple hypotheses, will you account for this?

We will use mixed effects models in a Bayesian framework and we will make inferences based on the posterior distribution of each fixed effect in our models. We will consider effects as “significant” when the lower and upper 95% credible intervals around the posterior mean do not overlap zero. We will test each of our hypotheses with a fit-to-purpose statistical model (see statistical analyses section for more detail). Because our models will be designed to test specific pre-registered hypotheses, we will not adjust effect sizes based on the number of hypotheses tested. We will report all results, regardless of the magnitude and direction of the effect sizes.

Data exclusion

How will you determine which data points or samples if any to exclude from your analyses?

How will outliers be handled? Will you use any awareness check?

We will work with all population and biodiversity time-series available through the Living Planet and BioTIME Databases^{24,25} that meet our inclusion criteria (see sample size rationale section). Our analyses focus on the marine and terrestrial realms; thus, we will exclude freshwater time-series. Both the Living Planet and BioTIME Databases have already been screened for errors and unrealistic values, thus any likely outliers have already been removed. We will not exclude any values, because we want to test what explains the variation across the full gradient of population and biodiversity change.

Missing data

How will you deal with incomplete or missing data?

The spatial resolution of the global change drivers we will use is global, thus we will be able to extract information on total human use, climate change, etc. for the locations of almost of our population and biodiversity time-series. The fishing data that are included in our human use data layer for the marine realm are incomplete towards the extremes of the southern and northern edges of the planet. For the marine realm, the driver data refer to the surface of the water (e.g., changes in sea surface temperature) as data from the ocean's depths are not currently available. For the time-series located at these southern and northern edges, we will assume that the commercial fishing pressure is zero, because those locations are very remote and the closest located pixels that do have fishing data have values very close to zero or zero.

We are aware that there are temporal gaps and mismatches between the population and biodiversity time-series and the global change driver data. Specifically, the durations of the time-series vary (Figure 5) and some of the time-series go back in time as far as midway through the 19th century. Global scale temporal data are not available for all of the anthropogenic drivers we are interested in, making it impossible to always match the duration of the population and biodiversity time-series with driver data from the same time period. However, the currently available global data do reflect the hotspots of human pressure around the world and reflect the best currently available opportunity to test the effects of global change drivers on populations and biodiversity at sites around the world. We will match the duration of the driver data with that of the population and biodiversity possible for the climate change layer and the forest loss layer, which is included in the human use data for the terrestrial realm. We will explore also matching the duration of the marine fishing data using the Watson 2017 database⁷¹. This dataset starts in 1950 and thus we can only use it for the subset of our time-series that begin after that time-period. For details on data choices for our global change layers and a discussion of their limitations, see Bowler et al. 2018²⁶.

Exploratory analysis

If you plan to explore your data set to look for unexpected differences or relationships, you may describe those tests here. An exploratory test is any test where a prediction is not made up front, or there are multiple possible tests that you are going to use. A statistically significant finding in an exploratory test is a great way to form a new confirmatory hypothesis, which could be registered at a later time.

We have conducted an exploratory ordination analysis of our data to better understand how well the locations of the population and biodiversity time-series represent the intensities of global change around the world (Figure 7). We compared the intensity of different global change drivers as well as their cumulative intensity between our study sites and simulated random global sampling. Overall, the population and biodiversity data we will use capture global variation in driver intensity, with the cumulative driver intensity variable explaining the most variation in exposure to anthropogenic pressure. The second most prominent axis of variation within both our data and the random global sampling was climate change.

We will mark any additional exploratory analyses as *post-hoc* tests.

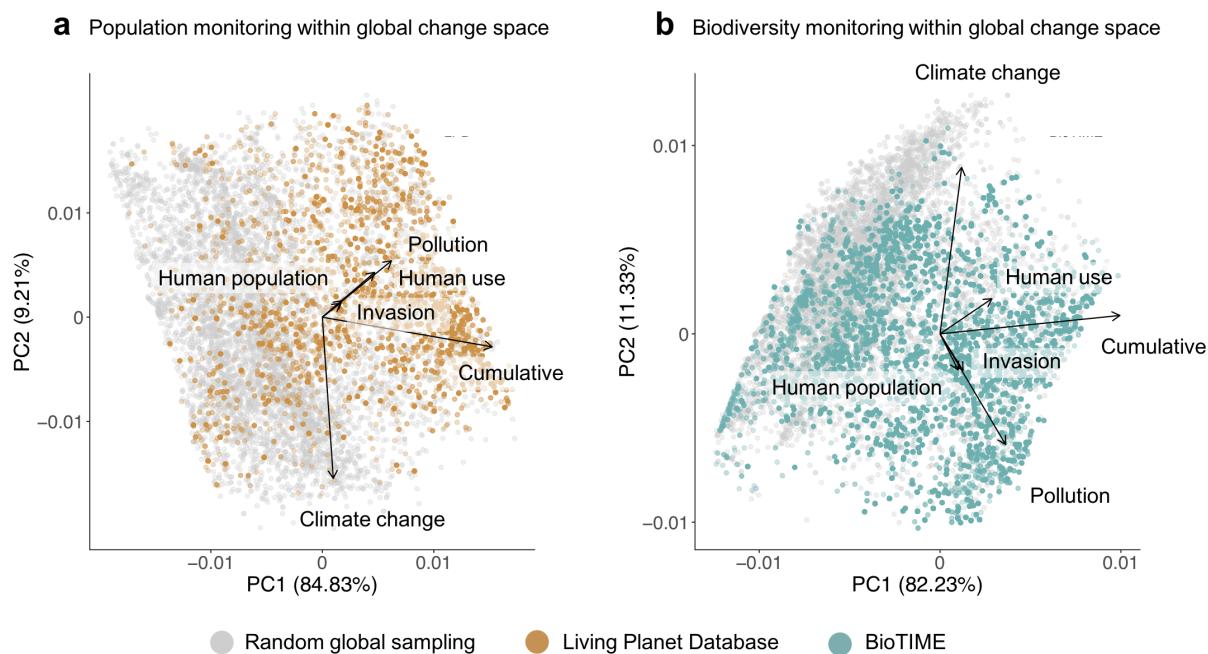


Figure 7. Population and biodiversity monitoring within global change space across the planet. Cumulative driver intensity captures most of the variation within driver intensity found at our study sites. The locations of population monitoring under-represent high climate change and low cumulative driver intensity, and the places with existing biodiversity monitoring under-represent high climate change intensities. The grey points are based on random sampling across the full extent of the globe.

Additional information

If there is any additional information that you feel needs to be included in your preregistration, please enter it here. Literature cited, disclosures of any related work such as replications or work that uses the same data, or other context that will be helpful for future readers would be appropriate here.

Our study is based on publicly available population and biodiversity data^{24,25} and thus the data are used other studies for a range of research questions.

As supplementary files, we include the R scripts for integrating the population, biodiversity and driver data and producing the figures in our pre-registration, as well as a sample script of our statistical models.

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