

**GLOBAL ASSESSMENT OF LOCAL BIODIVERSTIY CHANGES REVEAL SURPRISINGLY COMPLEX RESPONSES TO LARGE-SCALE HUMAN ACTIVITY**

*By*

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# Abstract/ Summary

Globally, biodiversity is changing in complex ways in a time of accelerating human impact. We lack real-world data how large-scale anthropogenic activity, as a prominent contemporary global change driver, is directly and indirectly influencing the reshuffling of ecological communities over time. Here, I quantify the influence of human activity captured with the metric accessibility to cities on ecological assemblages worldwide by analysing change in 5787 time-series across birds, mammals, plants and invertebrates. Surprisingly, I found that for every 10% increase in accessibility, species replacement (turnover) decreases by 5%. Turnover was highest for invertebrates and mammals and lowest for birds and plants. My findings demonstrate the complexity of real-world biodiversity change and challenge the assumption that current conservation focus on protecting wilderness areas might not be sufficient to achieve biodiversity composition conservation goals.

Linking human impact with biodiversity change can provide the needed evidence and predictions for better international policy making in the light of our rapidly changing Anthropocene.

questions current conservation priorities focussed on protecting wilderness areas.

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# List of abbreviations

CI Confidence Interval

BAIC Before after impact control

RQ Research question

# Introduction

**Background**  
Humans have modified 75% of terrestrial land cover, leading to major pressures on the biosphere and its inhabitants (IPBES, 2019). Growth of human population and the expansion of cities and road networks, which predicate the equity agenda of the UN by advancing accessibility (UN, 2015), are expected to intensify impacts on the natural environment (IPBES, 2019). Large scale human activity has altered abundance, richness and composition of ecological assemblages in complex ways (Dornelas *et al.*, 2014; Vellend *et al.*, 2017; Hillebrand *et al.*, 2018; Magurran *et al.*, 2018). The consequences on ecosystem processes and their resilience are not fully understood (Vellend *et al.*, 2017), yet biodiversity is increasingly instable (Hillebrand). Disentangling drivers of complex biodiversity change and establishing effective conservation practices without compromising human development is an urgent issue. Currently, we only have a limited quantitative understanding of how global change drivers, such as large-scale human activity, influence local patterns of biodiversity over time. Despite calls for more encompassing tests of the effects of global change drivers on biodiversity changes, research has mostly focussed on individual types of environmental change such as forest loss and land-use change. Recent global databases of large-scale human activity such as the accessibility to cities maps together with long-term biodiversity time-series allow us to quantitatively test more encompassingly global change drivers’ effects on biodiversity change. Linking large-scale human activity with biodiversity change can provide the needed information and predictions for better international policy making in the light of our rapidly changing Anthropocene.

Biodiversity changes depend on the scale and metric of observation (McGill *et al.*, 2015; Chase *et al.*, 2019). On a global scale, research points towards a detrimental impact of human activity on the natural environment with biodiversity declining, as is reflected in increasing global extinction rates. Contrary, on a local scale, biodiversity measured with the metric richness seems to be stable or even increasing (Butchart *et al.*, 2010; Dornelas *et al.*, 2014, ISla?). A potential explanation can be found when looking at the metric species turnover (changes in the composition of ecological communities), which can reveal changes in biodiversity that are often uncoupled from richness change (Dornelas). Communities seem to undergo replacement of some species by other species with no overall change in the total number of species. Although part of natural community persistence processes to some extent, current levels of turnover exceed baseline trends of existing ecological models (Dornelas, Magurran 18), with a likely connection to human impacts. This highlights that the biodiversity crisis is not about decline but rather about large-scale reorganization of communities leading to homogenization across space (Blowes *et al.*, 2019). This homogeneity leads to a decrease in biodiversity over larger scales and has serious implications on the ability of species communities to adapt to future environmental changes (Eriksson and Hillebrand, 2019). Thus, to comprehend biodiversity change across scales and make prediction for the future it is important to understand changes in communities’ compositions at the local scale.

Biodiversity change and its attribution to a specific driver can be assessed through different methods, each coming with its own advantages and disadvantages. Based on differences in methods used, local biodiversity changes driven by human activity are a topic of ongoing controversy. Research that use space-for-time and modelling approaches generally report negative trends of biodiversity change following human impact such as land-use change. Similarly, absence of human activity is reported as beneficial (Di Marco). Research that uses temporal trends and real-world data reports a more complex picture of biodiversity change with both negative and positive trends present. Space-for-time models can make use of much applicable data but have been criticised for the uncertainty in the assumption that time can be substituted for space. Especially when researching biodiversity change, this approach is lacking important temporal aspects such as ecological lags and community self-regulation with the consequent risk of overestimating the effect of global change drivers. Temporal assessments based on real world data can infer driver-response relationships by observing fluctuations through time. These attributions heavily depend on long-term availability and matching of data of both driver and response variables under observation. Assessing biodiversity changes and their relationship to global change driver could benefit from looking at real-world temporal data.  
  
Biodiversity change can be driven by multiple human impacts simultaneously. Humans have impacted the natural environment through a variety of activities such as habitat change, exploitation, pollution, climate change and introduction of invasive species. Previous studies have focussed on individual types of human impacts such as forest loss and land-use changes/transitions, which consequently attributed a very specific driver to biodiversity change. At the same time, these studies are limited in their extent to capture potential interactions of simultaneous human activities. To implement effective conservation measures it is not sufficient to look at one driver in isolation, but we seek to gain a more general understanding of biodiversity changes in reaction to large-scale human activities as we are dominating the planet. The metric accessibility to cities which is a measure of the closest travel time to the next urban centre can be seen as a proxy for multiple human influences. An increase in accessibility, goes along with increases of road network, urbanisation and human activities linked to urbanisation such as land-use changes and agricultural activity. This metric can capture changes to the environment and its inhabitants such as habitat fragmentation, land-use change, alien species and habitat loss as a cumulative measure. It allows to observe outcomes of potential interactions between those environmental changes, as they might interact additively, synergistically or antagonistically. Furthermore, it can be hypothesized that the impacts on biodiversity change might be amplified with higher exposure to human activities, driven by human population density. Biodiversity changes are influenced by simultaneous human activities which potential interaction effects between them and are thus captured better with a metric that accounts for a variety of human activities.

Biodiversity change is ultimately dependant on both the exposure to various drivers and species responses to environmental change (Foden, 2013). Species vulnerability varies with functional traits such as their life history, range-size and niche breadth and thus examining them separately for taxa can improve conservation strategy targeting. Species with small population sizes, high habitat specificity and restricted geographic extent are more likely to locally go extinct, thus increase the likelihood of biodiversity change. Less mobile species might struggle more to disperse and find a suitable refuge as there is more concentrated exposure to environmental change. Small population sizes are more prone to undergo stochastic fluctuations (Taylor’s power law) as well as higher occurrence of inbreeding with resulting reduced fitness. High habitat specificity means that colonization of new areas is restricted by limited habitat preferences. Species traits shared across a taxon make certain taxa more vulnerable to declines and extinctions. Studies looking at different species responses to a range of human impacts have found both positive and negative responses among taxa, related to functional traits. Understanding biodiversity changes on a taxa-specific level allows for more specific targeting of conservation efforts.

## Objectives and research questions

My aim is to quantify how global change drivers influence ecological communities over time. Specifically, I will focus on large-scale human activity captured in the metric accessibility to cities, and human population density and their relationship with temporal changes in community composition overall and across taxa. To achieve this, I investigate the influence of accessibility to cities on ecological assemblages worldwide and across taxa (birds, mammals, plants and invertebrates) by analysing change in 5787 time series, addressing the following research questions (RQ):

1. Do sites with higher accessibility to cities experience more changes in assemblage composition over time (temporal turnover) than locations with lower accessibility?
   1. How does the duration of ecological monitoring influence the magnitude of detected temporal turnover trends?
2. How is temporal turnover influenced by an interaction between human population density and accessibility?
3. How does temporal turnover of assemblage composition respond to levels of accessibility across taxa (birds, mammals, terrestrial invertebrates, terrestrial plants)?

## Research hypotheses

I hypothesize that there will be a positive relationship between higher accessibility to cities and greater temporal turnover. The magnitude of temporal turnover increases for sites which have been monitored over longer durations. The relationship between accessibility to cities and temporal turnover is steeper when human population density is higher. When looking at individual taxa, I hypothesize that taxa responses will vary for temporal turnover across levels of accessibility, with both positive and negative relationships present. Those hypotheses will be tested against the null hypotheses of no relationship between levels of accessibility and temporal turnover, no amplification of effect when human population density is higher and no difference in relationships between temporal turnover and accessibility across taxa.

## Predictions

I predict greater temporal turnover with greater magnitude of accessibility, as alterations of the natural environment caused by human activities facilitates colonisations of some species, while also leading to local extinctions. I predict greater temporal turnover in sites which have been monitored over longer durations, as the effect of turnover becomes more apparent over time. I predict the relationship between accessibility and temporal turnover to be steeper, when human population density is higher, as high human population density accelerates pressures on the natural systems, leading to higher turnover. I predict both positive and negative trends to be present among taxa, as they differ in functional traits and thus in their vulnerability to environmental changes.

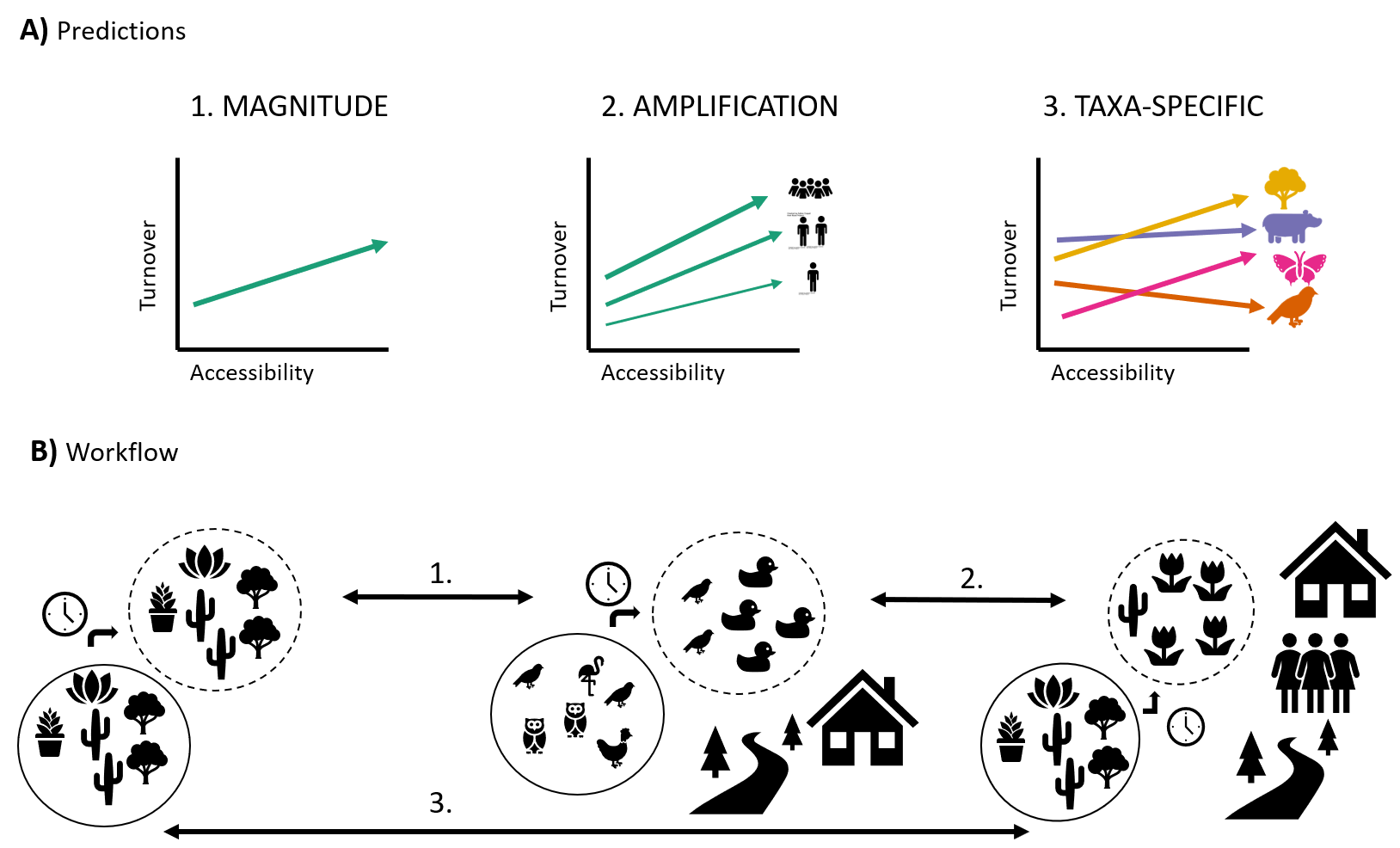
If I find support for my null hypotheses, this will indicate that the metric accessibility cannot sufficiently capture direct and indirect human impacts affecting biodiversity change, but also questions whether the current conservation emphasis to preserve wilderness areas is enough. If the results are in line with my alternative hypotheses, this will demonstrate the importance of humanly undisturbed places for the conservation of biodiversity.  
  


Figure 1. My study looks at three different aspects related to biodiversity change.  
**A** Conceptual diagrams of my predictions **B** Analytical workflow (figure inspired by Daskalova, 2019).

# Methods

In this study, I ask how 5787 ecological assemblages over time across four taxa (birds, mammals, invertebrates and plants) respond to levels of accessibility and human population density. To quantitively test the relationship of ecological communities and large-scale anthropogenic activity, I used 3 global databases.

## Databases

***BioTIME Database – biodiversity time series data***

I analysed 5787 time series from 181 different studies from 1023 unique terrestrial locations around the world, covering a range of taxa, including birds, mammals, invertebrates and plants (Dornelas *et al.*, 2018) that make up a part of the BioTIME database as of 12/03/2020. I did not predetermine sample size but used all available data that met my inclusion criteria: part of the terrestrial realm, minimum study duration of 5 years, at least 15 studies per taxa, no more than 5000 time-series per study, time-series fixed to one location and at least 2 survey points per time-series. Time-series that had no unique coordinates for their location, were located with the coordinates given by the study they belonged to. The resulting sample sizes across space, time and taxa can be found in Figure 2.

The time-series used represent repeated studies of species abundance and identity of all species found within an ecological community. The data collection of BioTIME was consistent within studies but not between studies.

Other research that used BioTime partitioned studies with large extent and consequently used sample-based rarefaction to standardise sampling within each time-series. Contrarily, I did not, as 64 % of my studies’ areas were equal to or smaller than 1km². 37 % of studies were located in protected areas. The duration varied across time-series, ranging from 1923 – 2016, with a mean duration of 19 years (standard deviation of +/- 13 years). Mean time-series per study were 64 (+/- standard deviation of 145).

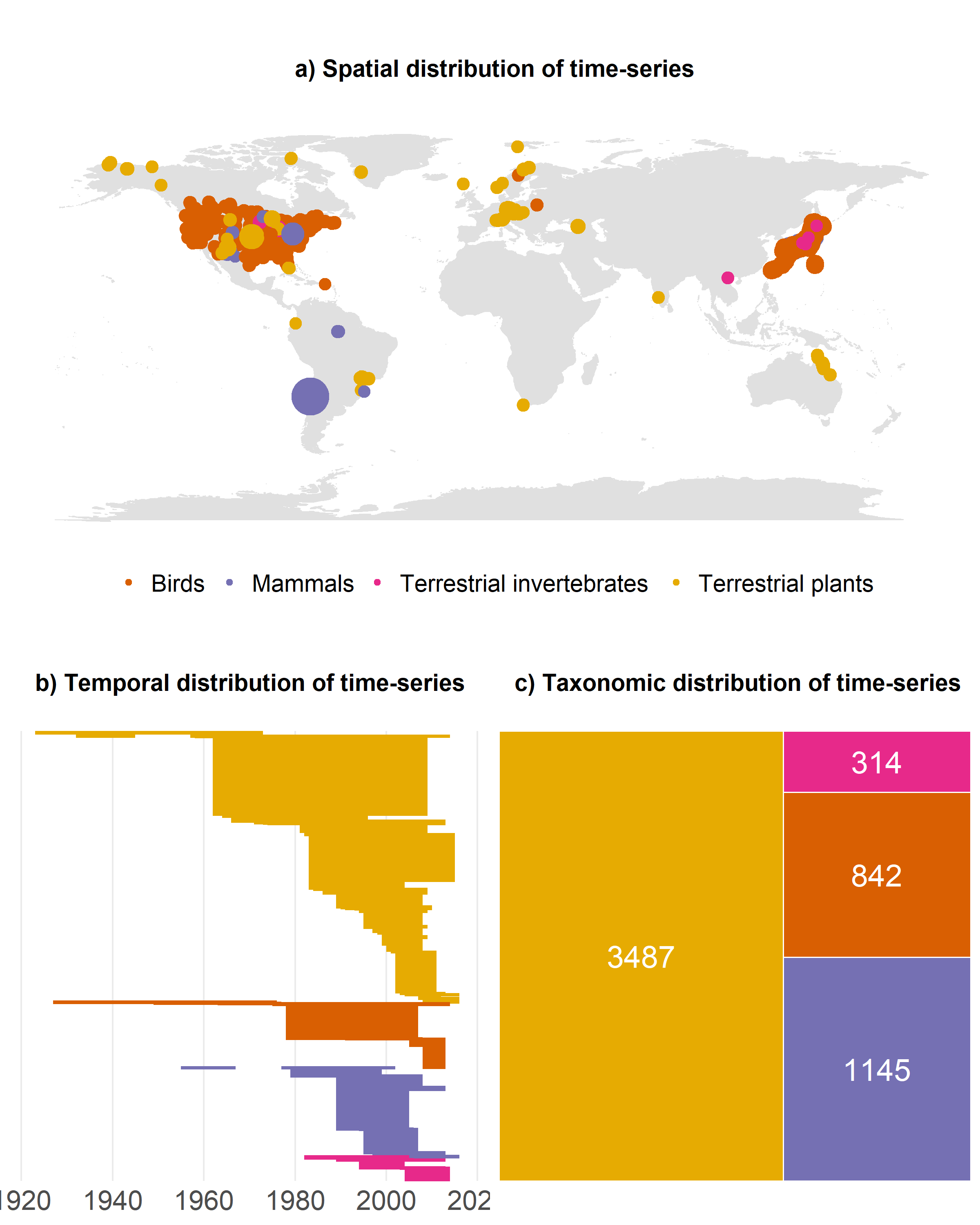


Figure 2. My study incorporates biodiversity time-series data across space, time and taxa (Figure inspiration Daskalova, 2019).

***Accessibility to cities 2015 data***To quantify large scale human impact, I extracted an accessibility to cities metric from the malariaatlas project Accessibility to cities 2015 global database. This database calculates least-cost-path land-based travel time to the nearest densely populated area (between 85 degrees north and 60 degrees south) at a 30 arc seconds resolution (approximately 1km at equator). Areas with >1,500 inhabitants/km² or a majority of built-up land cover types coincident with a population centre of at least 50,000 inhabitants are defined as densely populated areas. This dataset is available for the nominal year of 2015.

In the main figures, I used the inverses of travel time to nearest densely populated area, so that high values correspond to higher hypothesized human effect.

***Human population density dataset***  
To estimate human population density, I derived data from the Gridded Population of the World, Version 4: Population Density, Revision 11 database (CIESIN, 2018). Human population density was defined as number of persons per square kilometre, based on national censuses counts and population registers. Data is available at a 30 arc-second resolution (approximately 1km at equator). To match the timing of the accessibility dataset, I used the dataset for the nominal year of 2015.

## Data processing

All data processing was conducted in R v. 3.6.1. (REF R).

I quantified temporal changes in community composition within sites, as the turnover component of beta diversity (species replacement rather than abundance) at the last data point available relative to the first observation data point within each time-series using {vegan} and {betapart}. Turnover, as opposed to nestedness, was the dominant part of biodiversity change in the BioTIME dataset (REF). For study records that were not count data, I converted density and biomass records into presence/absence, so no data needed to be excluded. Temporal turnover is bound between zero and one, where zero is no change in community composition and one indicates that all original species have been replaced.

I harmonized both accessibility and human population density dataset to a standard global grid size of 25km² by taking the mean value of the grid cell when extracting the values with the {raster} package. I considered an area > 1km² to be more representative of the impact-influence relationship. My analyses were not sensitive to cell sizes over 25km² (tests from 25km² to 100km², but analysis showed higher values with similar slope for 1km²). I scaled the scores extracted between zero and one, where zero is not accessible/low human population density and one is very accessible/ high human population density.

To account for spatial autocorrelation, I created and assigned global grid cells to each time-series using {dggridr}. The grid cells covered areas of resolution 12, which is equivalent to an area of around 100km².

## Data analysis

I conducted all statistical analysis in R v. 3.6.1. (REF R). To quantify the relationship of accessibility and human population density across taxa on temporal turnover of ecological communities, I used mixed effects models in a Bayesian modelling framework based on a Stan computational framework and accessed through the {brms} package (REF). I based the models on a zero one inflated beta distribution to reflect the properties of turnover (bound between, and including, zero and one). I assumed a Bernoulli distribution for values of zero and one, and a beta error distribution for values between zero and one. I fitted the model with only an intercept.

I modelled temporal turnover as my response variable. Fixed effects were accessibility and duration of the time-series (RQ 1). I did not consider centring of duration necessary as the variation was relatively little within. Model convergence could not be achieved with the interaction term between accessibility and human population density, so latter was added as a fixed effect without the interaction (RQ 2). Neither could I achieve model convergence when allowing each taxon to have a random slope (nor intercept) with accessibility, so I added taxa as a fixed effect (RQ 3). I adjusted research question 2 and 3 accordingly when presenting my results and discussion. To account for confounding effects within the same study as the methods were consistent within but not among studies, Study ID was included as a random effect. To account for spatial autocorrelation the global grid cell variable was added as a random effect. I used {ggpredict} to calculate the model predictions. I assumed the said model set-up to be the optimal balance between requirements of the data and feasibility.

I used the default priors which are weakly informative as I had no ecological explanation to assume otherwise. The default priors can be found in the code in the appendix.I ran the models with 4000 iterations, with a warmup of 1000 iterations on 4 chains. I assessed convergence visually by examining trace plots and Rhat values (ratio of the effective sample size to the overall number of iterations. Values close to one indicate convergence.)

As I used a Bayesian framework, my inferences were based on the posterior distribution of each fixed effect. They were considered significant if the lower and upper 95% credible intervals (CI) did not overlap zero. I concluded all results, regardless of the direction or magnitude of the effect size.

The full R script, the link to the repository and to my preregistration and description of sensitivity analyses can be found in the appendix.

# Results

**Temporal turnover and accessibility (Research Question 1)**

Contrary to my predictions, I found that temporal turnover has decreased as accessibility increases across the 5787 time-series surveyed (slope = -1.20, CI = -2.09 to -0.32, Figure 1, see Table 1 for full model outputs). On average, for every 10% increase in accessibility, turnover decreases by 1.6 %. Notably, when taking the last census point as a baseline (lowest point of slope located at high accessibility), the ecological assemblages across levels of accessibility have experienced average 24% replacement of their species (as turnover is bound between 0 and 1) over their time-period monitored (average duration of 19 years). 63% of time-series experienced some turnover (turnover > 0) and only ~ 7% of time-series analysed experienced complete turnover of communities (turnover = 1). As 90.5% of data points have an accessibility score of 0.9 and above, there is higher uncertainty around the main effect at lower values of accessibility than at higher values, indicating the need to take the high value of temporal turnover at low accessibility with caution.   
  
In line with my predictions, the duration of the observation influenced the magnitude of the detected temporal turnover trends, with higher temporal turnover observed for longer monitoring of sites (see Figure A2 in appendix).

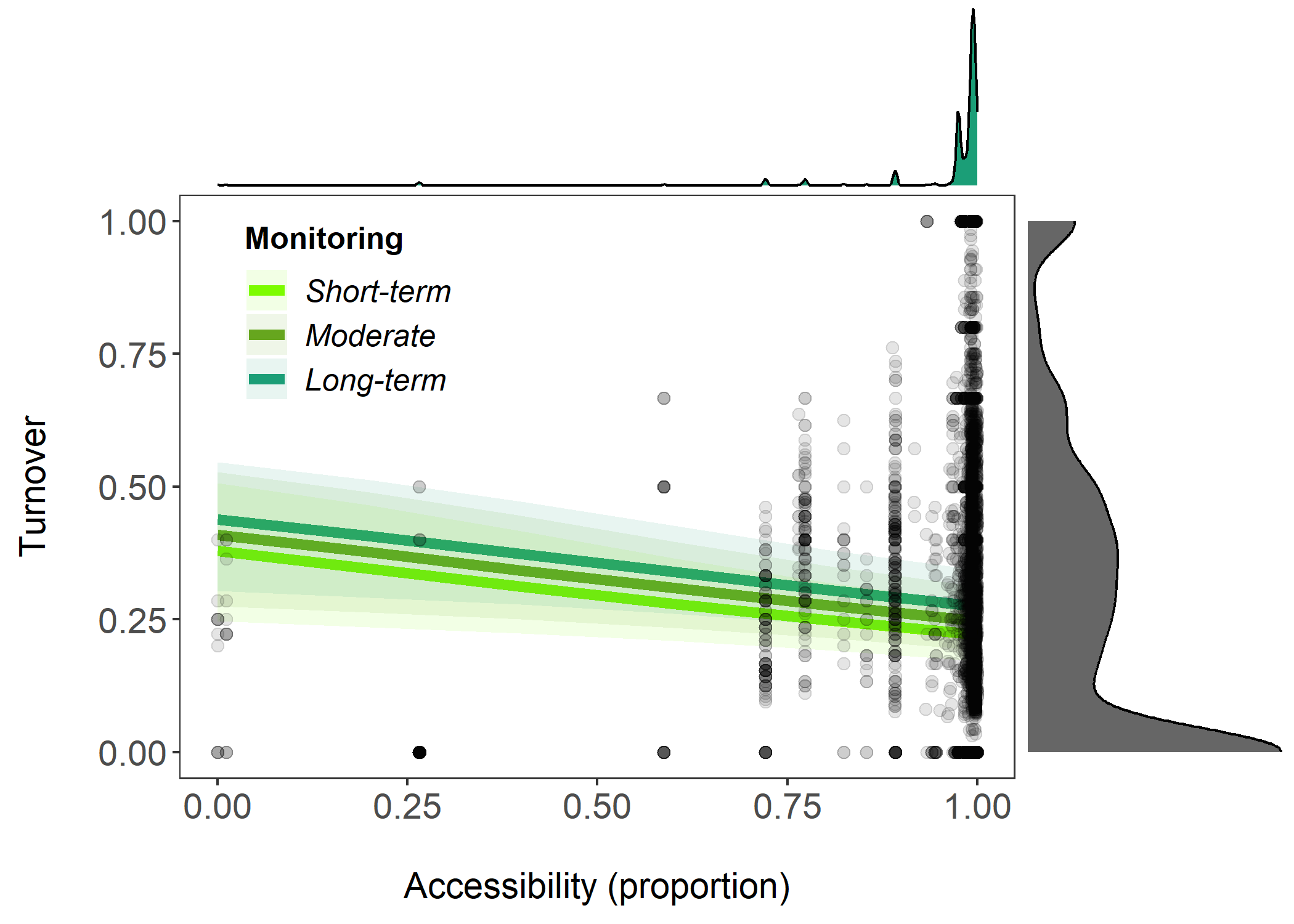


Figure 3. Temporal turnover has decreased as accessibility is increasing across the 5787 time-series surveyed (slope = -1.20, CI = -2.09 to -0.32, see Table 1 for full model outputs) using a mixed model. Grey points represent raw data. Lines and error bands represent model predictions and 95% credible intervals, respectively. Colour coding of lines represent differing duration of monitoring of time-series. The marginal density plots represent accessibility (top density plot) and temporal turnover (right density plot) distributions across all time-series surveyed. See trace plots and model Rhat values in appendix confirming model convergence.

**Temporal turnover and human population density (Research Question 2 modified)**

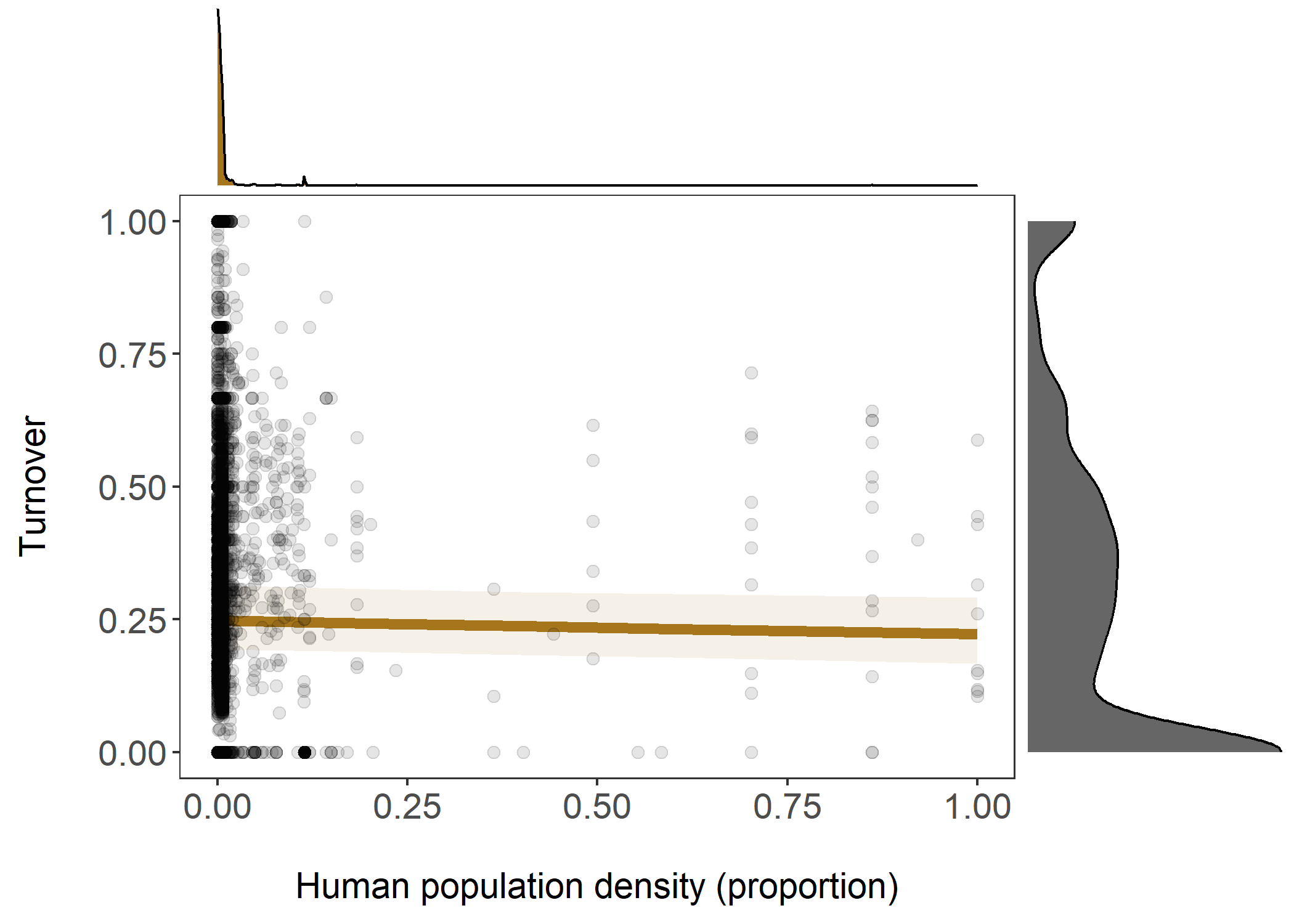
Looking at the relationship between temporal turnover and human population density (without the interaction as that model did not converge), I found that temporal turnover has neither increased nor decreased as human population density increases across the 5787 time-series surveyed (slope = -0.22, CI = -0.49 to 0.05, Figure 1, see Table 1 for more model outputs). Notably, when taking the last census point as a baseline (lowest point of slope located at high human population density), the ecological assemblages have experienced a 17 % replacement of their species (as turnover is bound between 0 and 1) over their time-period monitored (average duration of 19 years). Contrary to the distribution of accessibility falling into higher spectrum, 96.4% of data points have human population density score of 0.1 and below.   


Figure 4. Temporal turnover has showed no directional relationship with human population density across the 5787 time-series surveyed (slope = -0.22, CI = -0.49 to 0.05, see Table 1 for full model outputs) using a mixed model. Grey points represent raw data. Lines and error bands represent model predictions and 95% credible intervals, respectively. The marginal density plots represent human population density (top density plot) and temporal turnover (right density plot) distributions across all time-series surveyed. See trace plots and model Rhat values in appendix confirming model convergence.

**Temporal turnover and taxa (Research Question 3 modified)**

Looking at the relationship between temporal turnover and taxa (not considering the relationship across levels of accessibility as that model did not converge), I found that all taxa experienced temporal turnover (see Figure 5, Table 1 for full model outputs). Terrestrial invertebrates (slope = 0.99, CI = 0.31 – 1.7, n = 314) and mammals (slope = 0.71, CI = 0.01 – 1.42, n = 1145) experienced higher amounts of turnover relative to birds (slope = 0.11, CI = -0.87 – 1.14, n = 841) and plants (slope = 0, CI = -0.56 – 0.55, n = 3487). Terrestrial invertebrates experienced highest amount of turnover (0.54 times more than plants). The raw data demonstrates high variability of turnover experienced within mammals and lowest variability within birds. The number of time-series sampled for each taxon differed: of all time-series analysed 60% are made up of plants, followed by 20% mammals, followed by 14% birds and only 6% invertebrates. Out of the 37% time-series that showed no turnover at all, plants made up 73%.

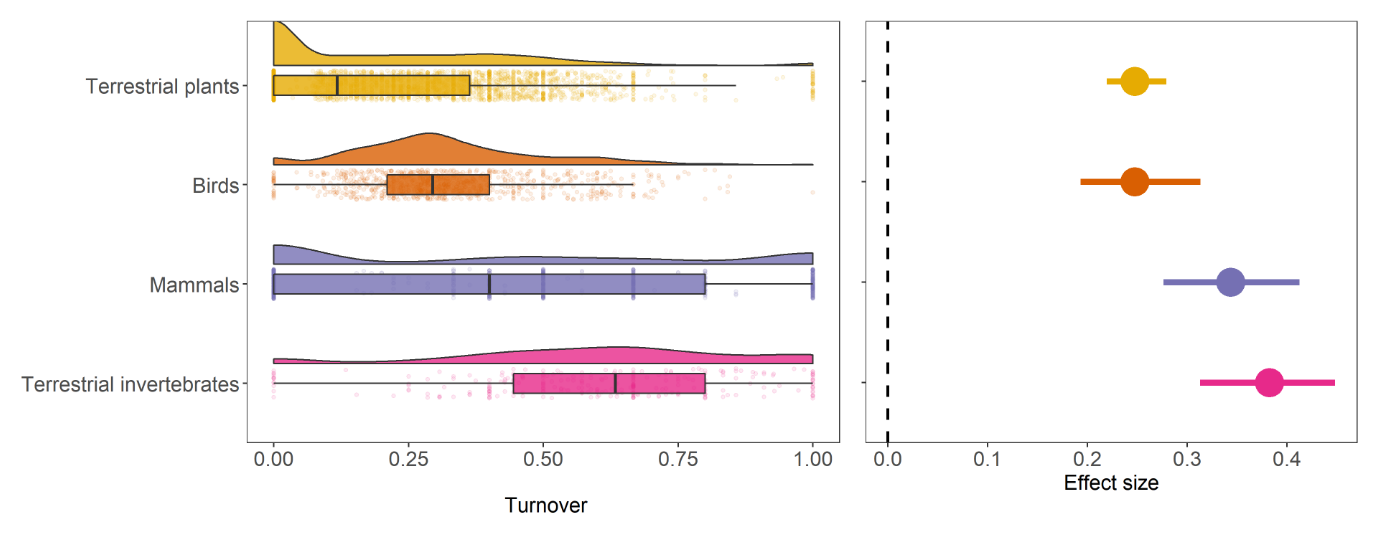


Figure 5. Temporal turnover is apparent across all taxa surveyed with variation among and within taxa using a mixed model. **A** Raw data visualisation of turnover across taxa. Split violins represent data distribution, boxplots with mean values and points are raw data. Numbers are sample sizes per taxon. **B** Model visualisation for temporal turnover and taxa. Terrestrial invertebrates (slope = 0.99, CI = 0.31 – 1.7) and mammals (slope = 0.71, CI = 0.01 – 1.42) experienced higher amounts of turnover relative to birds (slope = 0.11, CI = -0.87 – 1.14) and plants (slope = 0, CI = -0.56 – 0.55). Error bars represent 95% credible intervals. Dashed line marks the zero threshold. See trace plots and model Rhat values in appendix confirming model convergence.

# Discussion

**Overview**My global analysis of 5787 terrestrial time-series demonstrated complex heterogeneity in the relationships between large-scale human activity and biodiversity changes. Contrary to my predictions, I revealed that as accessibility increases, temporal turnover has declined (Figure 3), suggesting a rejection of my alternative hypothesis of a positive relationship. This highlights the importance of analysing multiple drivers and its interacting effects on biodiversity change. Simultaneously, I demonstrated that even the lower range of predicted temporal turnover rates are above baseline levels, highlighting widespread temporal turnover across levels of human activity (Figure 3). I found a very similar baseline magnitude of temporal turnover across levels of human population density, although in this case without any directional trend (Figure 4), pointing towards the importance of capturing both direct and indirect effects of human activities. I uncovered distinct taxonomic signals of temporal turnover, with terrestrial invertebrates experiencing the highest amount, followed by mammals, whereas plants and birds showed relatively lower levels of turnover (Figure 5). The lack of sufficient data prevented me to answer my original questions of an interaction between accessibility and human population. Similarly, I could not quantify the relationship between temporal turnover and taxa across levels of accessibility which highlighted the need for more comprehensive sampling in the future. On a global scale, human activities are causing a decline in biodiversity, but considering a more local scale I uncovered heterogenous responses to large-scale anthropogenic activity challenging the assumption that the absence of human activity is sufficient to conserve compositional biodiversity.

Global datasets have been criticised for various reasons with important implications for the interpretation of results. Firstly, critiques have denounced global biodiversity datasets of spatial underrepresentation of areas modified by human activities (Gonzalez), which prevents an accurate reflection of relationships between human modification and environmental changes. I found that the biodiversity monitoring in my subset of data covers a representative range of accessibility scores, as many parts of our planet are highly accessible (see appendix hist acc\_fake+real + map accessibility?). Contrarily, my data suffered from the opposite lack, as my data underrepresented areas with low accessibility, causing high uncertainty of the model at low levels (Figure 3). Additionally, it is important to note that 33% of the time-series monitored fell into protected areas while having an accessibility level of 0.9 and above (see appendix coloredbyPA). This means that firstly, protected areas are still exposed to human activities captured in the metric accessibility, but secondly that turnover rates at high levels of accessibility might be influenced by the presence of protected areas which are not strictly representative of other highly accessible areas. In a *post-hoc* sensitivity analysis, using a subset of plants-only data which showed most variation across levels of accessibility (see appendix figure raincloudacc), I found both similar directional relationships between accessibility and turnover, as well relatively high coincidence of time-series in protected areas (39%). Model convergence could not be achieved with a subset of data excluding protected areas, making it difficult to exclude this potential driver of turnover. The second criticism concerns mismatches in timing of disturbance and monitored time-series, as only then an attribution of a global change driver to biodiversity change is possible. One robust method to do this is the Before-After-Control-Impact method, which compares changes before and after disturbance. In my case, human activities related to accessibility have often occurred before the start of the biodiversity monitoring (REF) and neither did I have a quantification of large-scale human activities over time. Therefore, my results can be interpreted as the time-accumulated impact of human activities which captured both disturbances and recoveries at the same time and therefore gives a picture that is also representative of the real world (Vellend). Biodiversity change and its attribution to large-scale human activities is somewhat limited with my method used, however I still observed an accurate picture of the cumulative and interactive responses captured across levels of accessibility corresponded with human transformations of the natural environment, which is essential in predicting future biodiversity changes.

**Temporal turnover and accessibility (RQ 1)**

Additionally, there is evidence from the marine realm that when species are simultaneously exposed to multiple drivers, the resulting biodiversity effects are antagonistic and could produce patterns of no net biodiversity changes[**64**](https://www.biorxiv.org/content/10.1101/272898v5.full#ref-64). Invertebrate

Contrary to my first prediction, I found that temporal turnover has decreased as accessibility increases (Figure 3). I also found that 63% of all time-series monitored showed some degree of turnover (turnover > zero). Furthermore, the lowest model prediction at the highest level of accessibility pointed towards species replacement of 25% across the monitored time periods, which is higher than hypothetical baseline turnover rates (Dornelas). The negative relationship observed could be due to various reasons. Firstly, heterogeneity exists in species’ responses to impacts caused by human activities as is also reflected in the ongoing debate about habitat fragmentation, which will be explored later. Secondly, the potential interactions of multiple drivers play an important role. Accessibility is a cumulative variable, representing many different drivers and their respective environmental impacts. Most research has focussed only on a singular aspect of accessibility so far. Land-use change, urbanisation and roads are associated with both higher rates of extinction and immigration due to increasing alien potential (Hulme, [**2009**](https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10071#pan310071-bib-0030); Seebens et al., [**2015**](https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10071#pan310071-bib-0059)). However, many of the impacts described cooccur and can thus be affected by the intensity of one another (Geary, Nimmo, Doherty, Ritchie, & Tulloch, [2019](https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10071#pan310071-bib-0021)). Furthermore, simultaneous drivers can relate to each other in different ways, being either additive, antagonist or amplified (Cote, Darling, & Brown, [2016](https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10071#pan310071-bib-0008); Sirami et al., [2017](https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10071#pan310071-bib-0060)). We currently only have a limited understanding how the magnitude of exposure to these drivers differ. Research on multiple drivers on biodiversity change has been limited (Mazor et al., [2018](https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10071#pan310071-bib-0042); Sirami et al., [2017](https://besjournals.onlinelibrary.wiley.com/doi/10.1002/pan3.10071#pan310071-bib-0060)) with previous biodiversity change research mostly focussed on single drivers of environmental change such as forest loss, land use change and warming. Furthermore, other non-human activity drivers such as climate change can bring additional complexity in patterns of exposure as these drivers can cooccur and interact with human activity-related drivers as well (REFS). One determining coincidence of my study could be that the very inaccessible places I studied, coincide with areas that are in very high and low latitudes (often not very accessible) which experience more changes due to climate change and thus might show a higher level of turnover. My findings that accounting for multiple drivers and potential interactions is essential when attributing biodiversity change.

**Temporal turnover and human population density (modified RQ 2)**

I found a very similar baseline magnitude of temporal turnover and human population density as with accessibility, although in this case without any directional trend. The lowest model prediction at the highest level of human population density pointed towards a turnover level of 22% across the monitored time periods (Figure 4), making it very similar to the lowest level of turnover experienced across accessibility 24% (Figure 3), confirming a generally increased turnover rate above natural baseline levels. Interestingly, when looking at the coincidence of the distribution of accessibility and human population density, they were located on opposite ends (figure appendix histboth). That indicates that high accessibility does not come with high human population density but many places on earth have been modified even without the immediate or dense presence of humans. This is further emphasized by the finding that many highly accessible places coincide with protected areas (appendix graphprotectedarea). Therefore, accessibility seems to be an important measure to also capture indirect impacts. Much of our planet has been altered in such way that patches of habitat are exposed to both direct and indirect influences of human activity. While land-use change from pristine to urban centres and agriculture and forest loss represents more direct impacts, neighbouring habitats fragments are also impacted though more indirectly which might be reflected in a metric such as accessibility (Haddad, Waddle). As pointed out by Gonzalez, understanding and contrasting both direct and indirect effects of human activity on biodiversity change is a challenge that has not been addressed adequately yet. My findings highlight the importance of capturing both direct and indirect effects of human activities when attributing biodiversity change to global change drivers.

**Temporal turnover and taxa (modified RQ 3)**

My findings highlight variation of temporal turnover among taxa, with terrestrial invertebrates experiencing the highest amount, followed by mammals, whereas plants and birds showed relatively lower levels of turnover (Figure 5). Invertebrates relationship should be treated carefully, as the number of sampling was disproportionally lower (only 5% of time-series studied), disproportionally lower coincide with potential confounding effect protected areas (only 4% of invertebrates time-series studied) and known difficulties in sampling invertebrates (Andersen). Species’ responses ultimately depend on their traits such as life history traits, generation time, trophic levels and reproduction strategy (43,44 gerganga invertebrates). Concerning species’ vulnerability to human impacts and consequently setting conservation priorities, research often focussed on traits such as mobility/range size and specialisation/niche breadth. While some research has found more persistence of more mobile species and of species that are more generalist in human impacted areas (Newbold), other research has found both populations increases, and declines related to range size and specialisation (Gergana). However, both studies did not consider community composition in their analysis. Assuming birds as more-mobile species and plants as less-mobile species, and 90.5 % of time-series falling into a score of accessibility above 0.9 thus humanly impacted, I did not find a relationship between the range size and mobility. Despite there being no relationship with traits in this study, phylogenetic relatedness predicts extinction, occurring over longer timescales. Shorter timescales might be influenced by other processes such as the interaction of effects and ecological lags. I demonstrated heterogenous levels of turnover experienced among taxa, pointing out the need to quantify how these relationships are mediated by species’ traits and vulnerability in order to effectively target conservation efforts.

**Study limitations**

Analyses of biodiversity change can be limited by insufficient and imbalanced taxonomic, spatial and temporal data. The lack of model convergence which prevented me answering two of my original research questions highlight the need to collect data more comprehensively. Tropical locations and thus species were underrepresented in the biodiversity dataset (see figure 2), as were invertebrates in my subset of data. Spatial scales that are of species-specific relevance can differ heavily among species but also in relation to human impact. In a sensitivity analysis I found that turnover trends only differed in their magnitude but not in the direction of the relationship with accessibility and only between very small scales (1km²) but did no differ across bigger scales. Lastly, temporal mismatches and missing accurate accounts of past human activities make the attribution of biodiversity change challenging. Recognising heterogenous effects including disturbance and recovery of human impacts and focussing on understanding the interaction of current impacts are gaining importance even more. Analysis of biodiversity change and its global change driver can benefit from more comprehensive taxonomic, spatial and temporal data collection of environmental impact and biodiversity data.

**Future directions**

Biodiversity change and attributing global change drivers associated with human activities to it requires a step beyond previous studies which have focussed on singular drivers. Through exploring patterns of exposure of multiple influences (REF THREAT COMPLEXES) and analysing interactive effects of those various drivers, we can better understand the complex varieties with which our activities alter the environment and consequently ecological communities.

Biotic homogenization, marine realm

Look at taxa-specific response across exposure/levels of human impacts

# Conclusions

# By understanding how and why plant biodiversity has changed in recent centuries, we can improve predictions of how it will change in the future.

We caution that distilling the heterogeneity of local population change at sites around the world into a simple metric may hide diverging trends at local scales, where we found both increases and declines among species.

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My analysis reveals complex relationships of biodiversity change and large-scale human activities across taxa with a decrease of 1.6% of temporal turnover for every 10% increase in accessibility. These findings challenge the assumption that the absence of large-scale human activity is sufficient to conserve compositional biodiversity. Current assumptions are mostly based on space-for-time approaches. I join the latest research, calling for the importance of using real-world data to detect longer term dynamics that are revealing more complex biodiversity changes. I further highlighted the additional complexity in biodiversity changes arising through interactions between different drivers and environmental changes. To fully comprehend biodiversity changes it is not sufficient to consider singular environmental changes in isolation. A metric like accessibility although simple in one sense, cannot distinguish the relative contributions of each driver, thus more differentiated research in that direction is required. My findings, highlighting the complexity of biodiversity change as well as the heterogeneity in responses, challenge calls for establishing wilderness areas as a conservation priority, unless we gain a better understanding of current changes both inside and outside of human-impacted areas. Considering the full scope of biodiversity changes in response to and absence of large-scale human activities will improve predictions for better international policy making in the light of our rapidly changing Anthropocene.

# References

# Appendices

**Sensitivity analysis**I conducted sensitivity analyses to test potential limitations of my data. I ran an analysis of a subset of data that only included plants. Firstly, I conducted analysis to test the sensitivity of scale, modelling accessibility and human population density extractions of 1km², 50km² and 100km². Secondly, I ran a model with data included from only 1970-2015 to better temporally match the datasets to the nominal points of accessibility and human population density of 2015. Thirdly, in a post-hoc analysis I used a subset of my data that only included plants, as this was the taxon that was most equally distributed across levels of accessibility. All model terms were kept equal to the original model outlined above; except when I modelled plants, I removed the taxa fixed effect.

