Forest loss as a catalyst of population and biodiversity change

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Summary

Accelerating human impacts are reshaping Earth's ecosystems. Populations[1], richness[2–4] and composition[4] of communities at sites around the world are being altered over time in complex and heterogeneous ways[5–7]. Land-use change is thought to be the greatest driver of this population and biodiversity change in terrestrial ecosystems[8–10]. However, a major knowledge gap is whether land-use change drivers, such as forest loss and habitat conversion, can indeed explain the high heterogeneity of temporal population and biodiversity trends[9,11]. Here, we fill this gap by analysing change in 6,667 time series of populations (species' abundance)[12] and biodiversity (species richness and turnover in ecological communities)[13] over one and a half centuries of forest cover change and habitat transitions. We revealed an acceleration in both increases and decreases in population size, species richness and turnover after peak forest loss at over 2,000 sites across the globe. We found that temporal lags in population and biodiversity change following forest loss can extend up to half of a century and were longer for species with longer generation times such as large mammals. Together, our results demonstrate that historic and contemporary forest cover change do not universally lead to population declines and biodiversity loss, though population declines were most pronounced during and immediately following peak forest loss. By explicitly quantifying multi-decadal temporal lags in population and biodiversity responses to land-use change, our findings inform projections of how life on Earth will be reshaped across the Anthropocene.

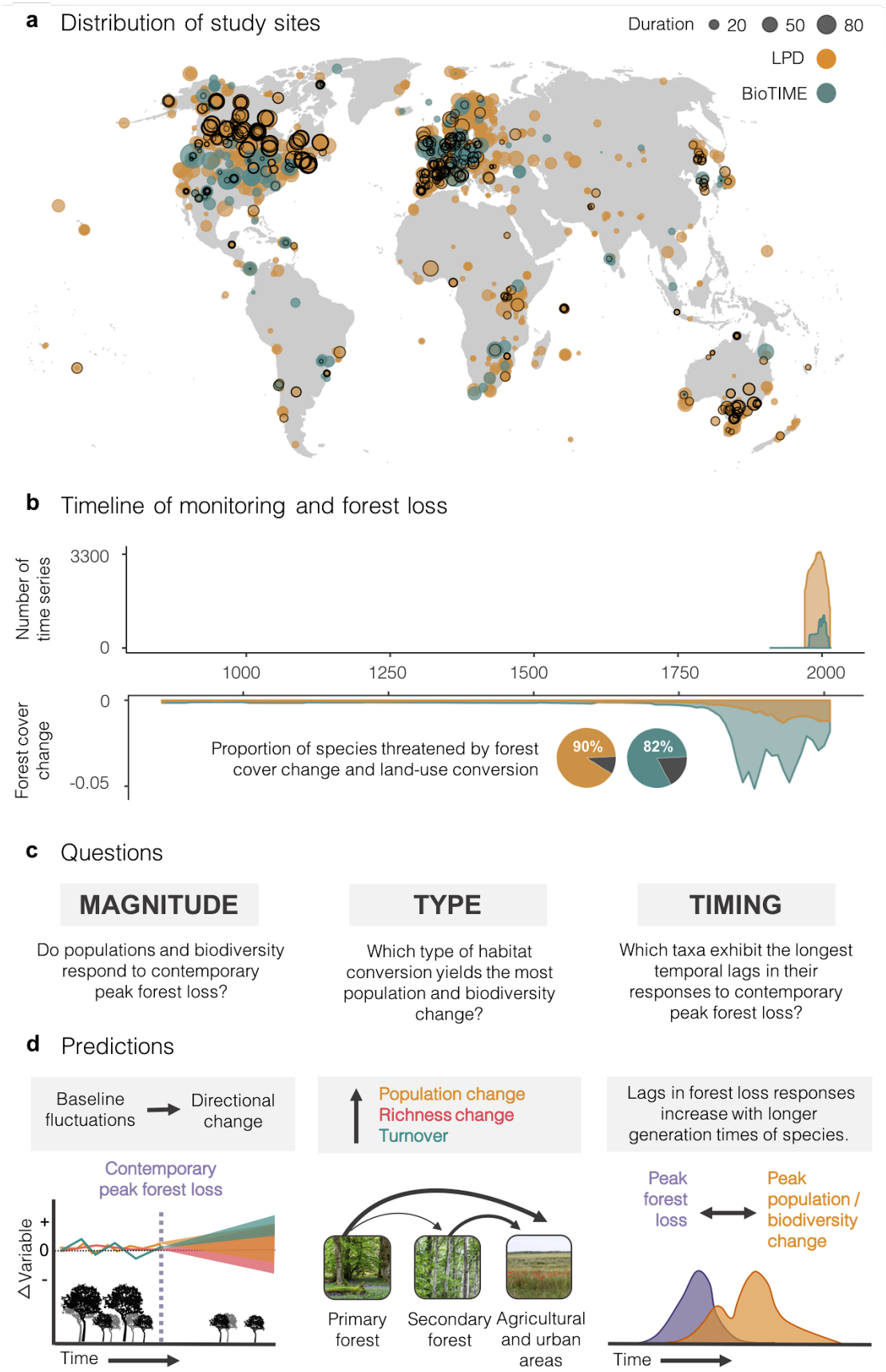
Main text

Earth's biodiversity is changing[3–5,14]. At sites across the planet, populations are increasing and decreasing[1,15,16], species are lost[17] and gained[18,19], yet synthesis studies across sites indicate no net change in local scale species richness[3,4] despite marked shifts in species composition (turnover)[2,4,5]. At present, we have only a limited understanding of how global change drivers

53 produce these complex population and biodiversity patterns over time[6,20,21]. Our current
54 knowledge of the mechanisms explaining the ongoing reorganisation of ecological communities
55 predominantly stems from space-for-time[8,22] and modelling[23,24] approaches that attribute
56 population and richness declines to land-use change. Yet, space-for-time methods can
57 overestimate the effects of global change drivers compared to long-term monitoring, because
58 they do not account for ecological lags[6,25,26] and community self-regulation[27]. Such temporal
59 discrepancies in the magnitude of effects have been observed when studying the impacts of
60 warming on community change[25], and of habitat fragmentation on populations and
61 biodiversity[28,29]. The integration of multi-century long reconstructions of past land cover[30] and
62 high-resolution remote-sensing observations[31,32] with recent compilations of over five million
63 population and biodiversity records[12,13] provides an unprecedented opportunity to test the *in-*
64 *situ* impacts of land-use change. Only now can we quantitatively attribute the heterogeneous
65 patterns of population and biodiversity change observed over time to land-use dynamics, thus
66 improving projections of human impacts on the world's biota.
67
68 Here, we asked how populations (trends in numerical abundance) and biodiversity (trends in
69 species richness and community composition) across vertebrate, invertebrate and plant taxa
70 vary according to the timing and magnitude of forest cover change and habitat conversions
71 (Figure 1, Extended Data Figures 1 and 3b). We assessed whether population and biodiversity
72 change were different after versus before contemporary peak forest loss (the timing of the
73 largest forest loss event across the duration of each time series). Additionally, we tested
74 population and biodiversity change versus overall forest cover gain and loss experienced across
75 the duration of each time series. In a *post-hoc* analysis, we categorized population time series
76 based on whether they were recorded before, during, or after the period of all-time historic peak
77 forest loss (the timing of the largest forest loss event at the location of each time series between

78 the years 850 and 2015), and then compared population trends among the three categories.
79 Finally, we investigated among-taxa variation in temporal lags of population and biodiversity
80 responses to peak forest (the time period between contemporary peak forest loss and maximum
81 change in populations and communities). We used a hierarchical Bayesian modelling
82 framework for all attribution analyses, with individual time series nested within biomes[33] to
83 account for the spatial and temporal structure of the data. We used the Living Planet Database
84 (133,092 records) and the BioTIME database (4,970,128 records), currently the two largest
85 databases of population and community time series, respectively. We calculated population
86 change using state-space models that account for observation error and random fluctuations[34].
87 We quantified turnover by partitioning Jaccard's dissimilarity measure into its nestedness
88 (change due to communities becoming reduced subsets of themselves or new species
89 colonising in addition to the original species) and turnover[35] components. We focused on
90 turnover because it quantifies compositional changes due to species replacement and is
91 independent of changes in species richness. Our data synthesis quantitatively tests the
92 attribution of change in populations and ecological communities to land-use change through
93 time across the world's woody biomes.
94
95 We predicted greater population and species richness declines with increased forest loss.
96 Forest degradation and land-use conversion reduce habitat and resource availability[8,19,36] and
97 are the most common global threats for our studied species[37] (Figure 1b, Extended Data Figure
98 4e). Conversely, we predicted greater increases in population abundance and species richness
99 with larger gains in forest cover. Forest restoration and natural regeneration, two examples of
100 forest cover gain, can lead to positive biodiversity responses[38,39]. We expected greater turnover
101 of species within ecological communities with greater change in forest cover (both loss and
102 gain), as these extremes of the forest cover change spectrum both create novel environmental

conditions prompting local extinctions but also colonisations by new species[27,36]. Secondly, we predicted that the largest population declines will occur during the periods of all-time peak forest loss across sites as that is the baseline for maximum intensity of forest cover change[26]. Finally, we predicted that temporal lags will be greater for species with longer generation times, as they typically respond more slowly to environmental change[40] and have more limited dispersal[41]. If we find support for our overall prediction that population and biodiversity loss will be greater with higher forest loss, this would indicate that forest loss is a key driver of rapid and pervasive declines over time. Alternatively, if we find support for heterogeneous and temporally-delayed responses of populations and ecological communities to forest loss, this would imply that the effects of land-use change over time are more complex than previously thought, which has implications for improved prediction of future ecological change and development of biodiversity and conservation policy.


a Distribution of study sites
Duration 20 50 80
LPD
BioTIME
b Timeline of monitoring and forest loss
Number of time series
3300
0
1000
1250
1500
1750
2000
Forest cover change
0
-0.05
Proportion of species threatened by forest cover change and land-use conversion
90%
82%
c Questions
MAGNITUDE
Do populations and biodiversity respond to contemporary peak forest loss?
TYPE
Which type of habitat conversion yields the most population and biodiversity change?
TIMING
Which taxa exhibit the longest temporal lags in their responses to contemporary peak forest loss?
d Predictions
Baseline fluctuations
Directional change
Population change
Richness change
Turnover
Lags in forest loss responses increase with longer generation times of species.
Contemporary peak forest loss
ΔVariable
+
0
-
Time
Primary forest
Secondary forest
Agricultural and urban areas
Peak forest loss
Peak population / biodiversity change
Time

115

Figure 1. Forest cover change can influence population and biodiversity change through multiple mechanisms. For 38% of population time series and 70% of biodiversity time series monitoring began after historic peak forest loss had already occurred (see Extended Data Figures 2-3, 4a-b). See Extended Data Figure 1 for workflow of analyses. **a,** Global map of locations and duration of 542 Living Planet Database (LPD) and 190 BioTIME studies, containing the 6,497 time series from 2,154 locations analysed here. From the total number of time series analysed, 2,852 had experienced historic or contemporary forest cover gains and losses. Black outlines on **a** indicate locations that were forested at the start of the population or biodiversity monitoring period (1,247 sites). **b**, Timeline of monitoring and forest loss across the LPD and BioTIME databases (for variation in monitoring duration among time series, see Extended Data Figures 2-4). Forest loss was quantified over 10-year periods across 96 km^2 cells as a proportion, with e.g., -0.05 meaning a 5% loss of forest cover. Inset on **b** shows the proportion of species, part of the LPD and BioTIME databases, that are threatened by land-use change, based on species' IUCN threat assessments (see Extended Data Figure 4e). **c-d**, Questions and predictions for this study outlined with respect to population change, richness change and turnover (species composition change). Habitat conversion refers to a change in the dominant land cover type. Photos in **d** are by G. N. Daskalova.

We found that forest loss and habitat transitions did not universally lead to population declines and biodiversity loss (Figures 2-3) and are instead reshaping populations and ecological communities in more complex ways than previously recognised[8,15,22,24]. Surprisingly, forest loss acted as a catalyst for both positive and negative change and intensified population declines, population increases and species richness losses over time, despite equally long monitoring periods before and after peak forest loss. In 72% of the populations which were in decline before peak forest loss, the declines became more acute after forest loss (slope = -0.04 CI = -0.04 to

-0.03, Figure 2a). Similarly, 66% of the increasing populations experienced even more positive population change after peak forest loss (slope = 0.02, CI = 0.02 to 0.03, Figure 2b). In contrast, among time series, we did not find directional relationships among greater forest loss and population and species richness declines (Figure 3, Extended Data Figures 5-7). This disconnect between the magnitude of land-use change and population and biodiversity change could be due to a number of factors including temporal lags in population or community responses[26,40] and/or less forest cover change having occurred during the monitoring period relative to historic forest clearing[26,42,43] (Extended Data Figures 2-3). In further contrast to our first prediction, larger magnitudes of forest loss often led to greater increases, rather than decreases, in species richness over time, particularly among time series comparisons with shorter durations (Extended Data Figure 6e). Forest loss is a key driver of habitat fragmentation which can lead to rapid colonisation by new species due to increased landscape heterogeneity and larger breadth of ecological niches across sites[5,28,36]. Our results highlight that the same global change driver, forest loss, affects populations and ecological communities in heterogeneous ways at different sites around the world, and accounting for this heterogeneity is key when scaling from local impacts of human activities to global scale biodiversity patterns and attribution of change[10].

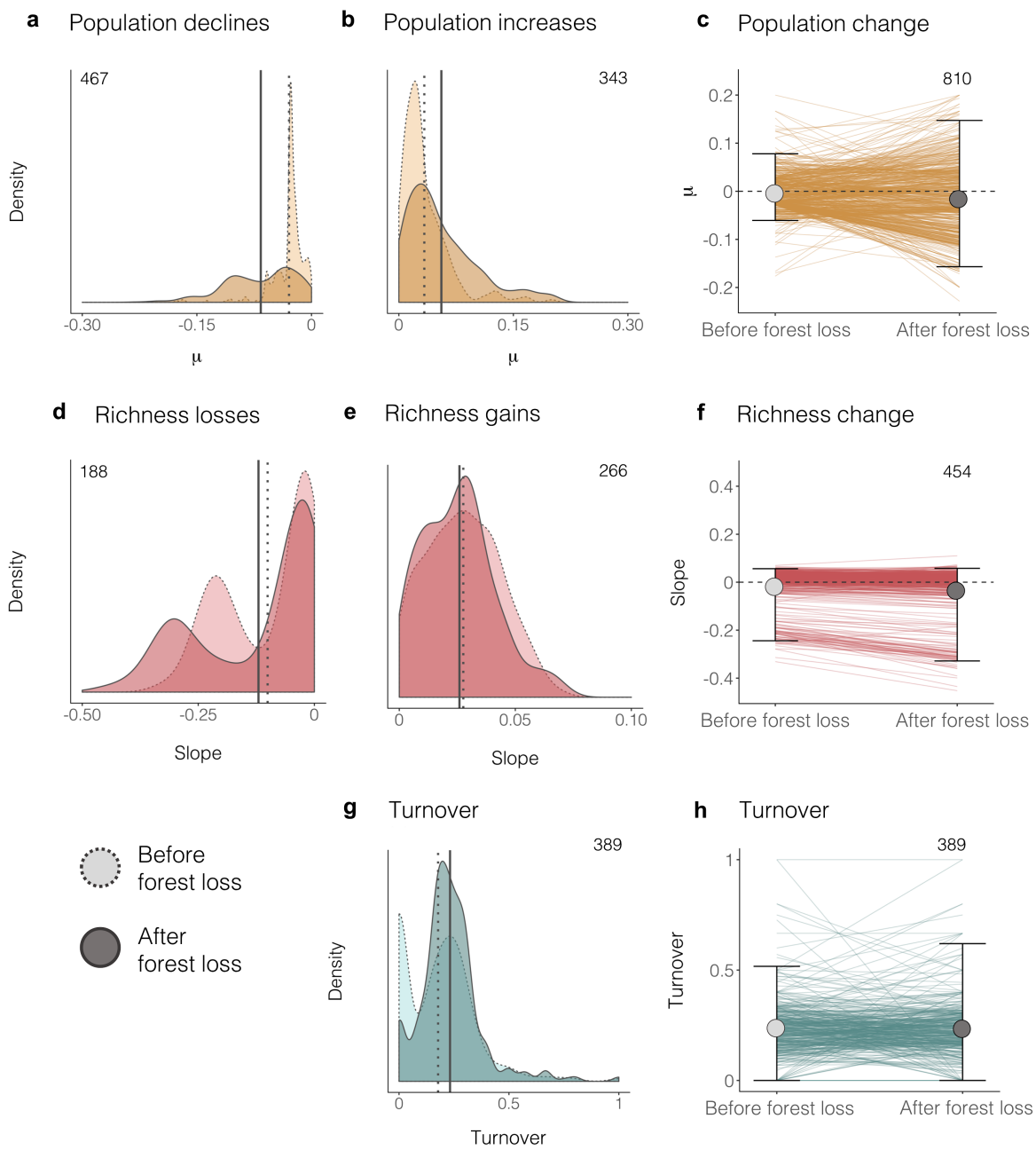


Figure 2. At the site level, population and biodiversity change increase after contemporary peak forest loss. Though species richness tended to decrease after peak forest loss, the proportion of populations that experienced increases and declines in population abundance and turnover were similar. Numbers on plots indicate number of time series. Population, richness and turnover change increased across 55% of the 1,007 time series for

which baseline comparisons were possible. Distributions show posterior means from model fits of **a**, population declines (μ), **b**, population increases (μ), **d**, richness losses (slopes), **e**, richness gains (slopes) and **g**, turnover (in the final year of each period relative to the first year, measured as Jaccard's dissimilarity, where zero indicates no changes in species composition and one indicates a completely new set of species). Vertical lines indicate the mean for each category. The y-axis on **a**, **b** and **c** refers to the probability density function for the kernel density estimation per unit on the x-axis, and the distributions are relative to one another. Temporal change before and after peak forest loss, **c**, **f**, **h** is indicated with lines for individual time series. The time window duration varied among time series but was consistent at the time series level (*n* years before disturbance = *n* years after disturbance at the time series level, n ≥ 5 years). Light grey and dark grey points indicate the mean values across all times series, with error bars indicating the 2.5 and 97.5% quantiles. See Extended Data Table 1 for model outputs.

Our results revealed that population declines were most pronounced during the period of all-time peak forest loss and turnover was highest when primary forests were converted to agricultural and urban areas (Figure 3). Following peak contemporary forest loss, turnover increased by over 10% in 19% of the time series (Figure 2), further testifying to the high rates of compositional change detected across the Anthropocene[4,5,14]. However, within 22% of the time series, turnover declined by over 10% after forest loss, suggesting that biotic homogenisation might also be occurring following human-induced environmental change[44]. Taken together, our findings suggest site-specific impacts that were stronger and more common when the population and biodiversity monitoring captured the largest forest loss events and the most dramatic habitat conversion events across time relative to when monitoring is mismatched with forest cover change (Figures 2-3). A greater proportion of the planet is projected to experience an unprecedented amount of land-use change in the coming decades[45], highlighting

the importance of improved biodiversity monitoring in current and future hotspots of forest loss and habitat conversion.

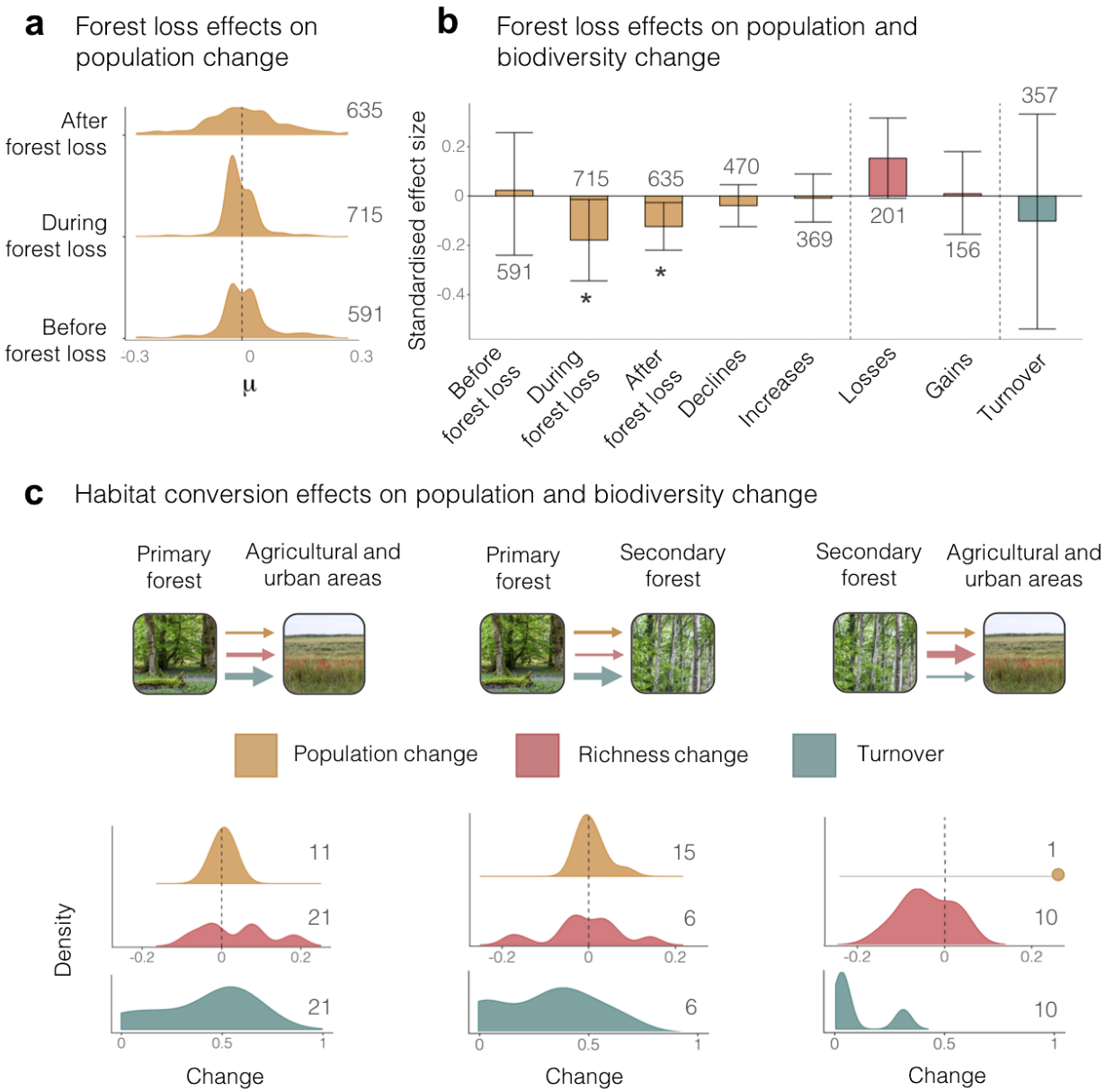


Figure 3. Population declines were most acute when the all-time peak in deforestation for study sites occurred within the duration of population monitoring. a, Population declines are more likely to be detected when peak deforestation occurs during the population monitoring period (slope = -0.01, CI = -0.01 to -0.01). Density plots show distributions of μ values

196 (population trend). **b,** Among time series, there were no directional relationships among overall
197 forest loss and population declines and increases, species richness declines and turnover.
198 Standardised effect sizes in **b** were calculated by dividing the slopes from hierarchical models
199 testing population and biodiversity change as a function of forest loss by the standard deviation
200 of forest loss. For visualisations of each model, see Extended Data Figures 5-6. Low sample
201 size precluded an analysis of biodiversity change differences based on whether all-time peak
202 forest loss had occurred before, during or after the biodiversity monitoring. Distributions in **c**
203 show μ values for population change, posterior means (slopes) for richness change and
204 Jaccard's dissimilarity for turnover under different habitat conversions. Line thickness
205 corresponds with magnitude of detected change. Forest loss led to habitat conversion in 304 of
206 5795 (approximately 5%) of monitored population and biodiversity time series. There was only
207 one instance of a population time series experiencing habitat conversion with secondary forest
208 as the starting dominant land cover, thus no distribution is plotted for that category. The y-axis
209 in **c** refers to the probability density function for the kernel density estimation per unit on the x-
210 axis, and the distributions are relative to one another. Numbers in plots indicate number of time
211 series for each category. Small sample sizes of an average 10 time series per transition types
212 of interest for this analysis precluded statistical analysis and inferences on the effects of habitat
213 transitions were drawn by visually inspecting the density distributions. See Extended Data
214 Figures 5-6 and Extended Data Table 1 for models of forest cover gain and loss (GFC
215 database[12], 2000-2016) and forest cover loss (LUH database[11], across the time series) and
216 population and biodiversity change. See Extended Data Figure 7 for distributions of population
217 and biodiversity change following habitat transitions detected by the MODIS Land Cover
218 Database[32].
219

We found evidence for up to half-century ecological lags in changes in population abundance, species richness and community composition following forest loss (Figure 4). On average, we documented maximum change in populations and biodiversity six to 13 years after contemporary peak forest loss across taxa. Yet, nearly half of population and biodiversity change (40%) occurred within three years of peak forest loss, demonstrating that rapid shifts in populations and ecological communities occur frequently (Figure 4a). As predicted, the period between peak forest loss and peak change in populations and biodiversity was longer for taxa with longer generation times (e.g., large mammals, Figure 4b, Extended Data Table 1), further confirmed by a *post-hoc* analysis of lags in population change versus mammal generation time (Extended Data Figure 8a). Population declines and increases occurred on similar time scales (Extended Data Figure 8b-c), potentially explaining why previous temporal analyses of population change have not found evidence for net population declines[1,20]. Losses in species richness lagged behind richness gains only by approximately half a year (slope = 0.5, CI = 0.1 – 1.05), indicating that potential extinction debts and immigration credits accumulated at roughly the same speed across taxa. The similar pace and temporal delay of richness gains and losses could be the source of the previously observed findings of no net local richness change[3,4], yet substantial compositional change[2,4] across sites and taxa. Such temporal lags in biodiversity change have also been observed in post-agricultural forests[2,46] and fragmented grasslands[40], where agricultural activity has ceased decades to centuries ago, yet richness and community composition change continue to the modern-day. Overall, our results indicate that increasing rates of land-use change in the Anthropocene[11,45] will alter ecosystems on both short- and long-term timescales.

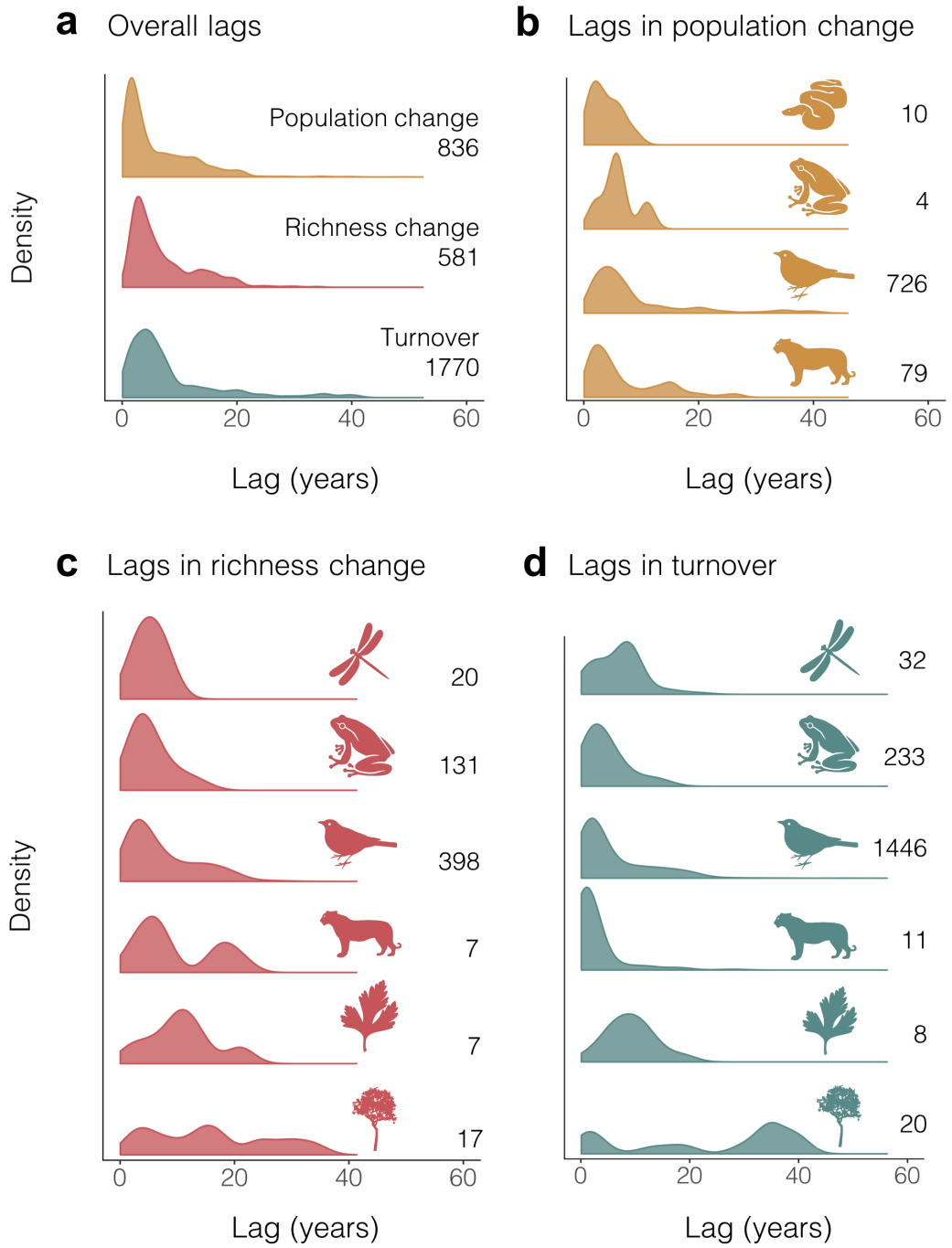


Figure 4. Population and community change after peak forest loss may be delayed by up to half a century across 3,187 time series from around the world, with species with long generation times and low mobility showing the largest temporal lags. a, Distributions of

temporal lag values (measured in years). **b,** Vertebrate population change lags by taxa (reptiles, amphibians, birds and mammals). **c,** Richness change and **d**, turnover lags by taxa (invertebrates, amphibians, birds, mammals, plants and trees). Peak forest loss refers to the timing of the largest forest loss event across the duration of each time series. Lag was measured as the number of years between peak forest loss and peak population/biodiversity change. Turnover was measured as Jaccard's dissimilarity, where zero indicates to changes in species composition and one indicates a completely new set of species. Numbers on plots indicate number of time series. Some time series did not experience richness change following peak forest loss, thus no lags were calculated for them. See Extended Data Table 1 for model outputs.

In summary, our analysis reveals an acceleration of increases and decreases of populations and biodiversity after forest loss and habitat conversion at sites around the planet. Our findings that all is not loss contrast with our hypothesis and challenge the widely-held assumption that land-use change universally leads to population declines and species richness loss[8,15,23]. Nevertheless, the increased magnitude and likelihood of population declines during and following peak forest loss highlight that human impacts are altering the biodiversity of the planet and emphasize the importance of expanded biodiversity monitoring in current and future hotspots of land-use change. A critical assumption underlying existing projections of biodiversity responses to land-use change[8,23] is that space-for-time approaches accurately reflect longer-term population and biodiversity dynamics[11]. On the contrary, we find that temporal lags in population and biodiversity change following forest loss varied by taxa and generation time and extended up to half of a century. Over the Anthropocene, ecosystems could be responding to a suite of global change drivers, in addition to land-use change, and a key next research step is to test the synergy and discord between the effects of multiple anthropogenic threats on Earth's biota. Our results highlight the complex biological responses to habitat conversion across sites,

taxa and time scales that are leading to the reorganisation of ecological communities. Thus, indicators used to assess biodiversity change regionally and globally[10], including progress towards Aichi targets[47], must capture the full spectrum and temporal spread of population and biodiversity responses to human impacts across the Anthropocene.

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Author contributions

G.N.D., M.A.D. and I.M.S. conceptualised the study. G.N.D. integrated databases and conducted statistical analyses with input from S.B., I.M.S., A.D.B. and M.A.D. G.N.D. created the figures with input from co-authors. S.B. and S.S. wrote the code for the rarefaction of the BioTIME studies. I.M.S. was the primary supervisor and M.A.D. the co-supervisor for G.N.D. M.A.D. and A.M. funded the compilation of the BioTime database. G.N.D. wrote the first draft and all authors contributed to revisions.

Methods

For an illustration of the workflow of our analyses of forest cover and population and biodiversity change through time, see Extended Data Figures 1 and 3b. All data and statistical analyses are described in detail below. We did not predetermine sample size and instead worked with all available temporal population, biodiversity and forest cover change data that met our duration criteria. For analyses of population change, we included time series with five or more survey points. For analyses of biodiversity change, we included time series with five or more data points when analysing the full time series, and time series with two or more data points when matching the duration of time series comparisons to the 16-year duration of the Global Forest Change Database from 2000 to 2016).

422

423 **Databases**

424 *Forest cover change data*

425 To quantify historic and contemporary forest cover change, we extracted historic forest loss
426 from the Land Use Harmonisation (LUH; 850 – 2015, forest loss and habitat transitions at a
427 0.25° degree resolution)[30] and contemporary forest cover change and habitat conversions from
428 the Global Forest Change (GFC, 2000 – 2016, forest loss and gain at a 30 m resolution)[31], and
429 MODIS Landcover (2000 – 2013, land-use transitions at 500m resolution)[32] datasets.

430

431 *Land Use Harmonisation Database*

432 To estimate forest cover change across a time period matching the full duration of the
433 biodiversity observations, we derived the change in primary forest cover from the Land Use
434 Harmonisation database (LUH)[30] for 96 km^2 cells around the location of each population in the
435 LPD database and for the standardised grid cells of the BioTIME database (~ 96 km^2 each).
436 LUH includes annual gridded fractions of land-use states for the period from 850 to 2013 at
437 0.25° x 0.25° resolution. The estimates are based on historical reconstructions using Earth
438 System models, with inputs such as regional and national rates of wood harvest and potential
439 biomass density. The accuracy and precision of LUH increases towards the modern day, when
440 there are more available data to inform the Earth System models. Note that unlike GFC, LUH
441 estimates forest cover as a proportion (bounded between zero and one). For our analyses, we
442 focused on time series from locations that have experienced at least 0.05 (equivalent to 5%)
443 forest loss. To calculate total forest cover change over the period of a given population or
444 biodiversity time series, we subtracted the proportion of forest cover in the first year of
445 biodiversity monitoring from the proportion of forest cover in the last year. The type of forest
446 cover change detected by the LUH database was predominantly forest loss, with forest gain

447 occurring infrequently and at very small magnitudes (<0.001 out of maximum 1), thus we focus
448 our analysis on forest loss.
449
450 To estimate the historic baseline of forest cover change, we calculated yearly change in % forest
451 cover in a study cell from one year to the next for each site from 850 to 2015 from the LUH data,
452 and determined the 10-year period when the most forest loss occurred (historic peak forest loss,
453 calculated by adding the yearly proportions of forest loss in each cell over standardised 10-year
454 blocks). Time since historic peak forest loss was a poor predictor of the variation in
455 contemporary population and biodiversity change (Extended Data Figure 10e-f). To determine
456 contemporary peak forest loss for each time series of monitoring data, we calculated yearly
457 changes in forest cover across the duration of each time series and determined the year when
458 the most change had occurred.
459
460 *Global Forest Change Database*
461 We derived overall forest loss and forest gain across the 2000-2016 period for 96 km^2 cells
462 around the location of each population in the LPD database and for the standardised grid cells
463 of the BioTIME database (~ 96 km^2 each) from the Global Forest Change (GFC)[31] database
464 using the Google Earth Engine[48]. The GFC database provides high resolution forest cover
465 change data, derived from Landsat satellite observations at a 30-meter spatial resolution. We
466 calculated the total area of forest cover gain and loss separately (measured in km^2) for each 96
467 km^2 cell on a yearly time step. We then summed the yearly values for the period that coincided
468 with population and biodiversity monitoring to estimate overall forest cover gain and loss (two
469 separate metrics). For example, for a biodiversity time series spanning 2002 – 2009, our forest
470 cover gain and loss metrics included the total amount of forest cover gained and lost during that
471 same period. For our analyses, we focused on time series from locations that have experienced

472 at least 0.5 km^2 of forest gain or loss. GFC does not distinguish between primary forest,
473 secondary forest and plantations, but it does provide a very high-resolution measure of general
474 forest cover. The drivers of the forest loss detected by GFC across our study sites are
475 predominantly forestry, changes in agricultural practices and wildfires[49]. Note that the GFC
476 database spans from 2000 to 2016, whereas the earliest terrestrial biodiversity record in
477 BioTIME is from 1858.
478
479 *MODIS Landcover Database*
480 We used the MODIS Landcover Database[32] to quantify habitat conversion for locations where
481 we had population and biodiversity monitoring data. The MODIS Database has a resolution of
482 500 m, and it uses satellite-derived reflectance data to classify land cover around the world. To
483 determine the types of habitat conversion between 2000 and 2013 (the time span of available
484 MODIS data) across all monitoring locations, we calculated the dominant land cover type at the
485 start and end of each population and biodiversity time series and split time series into categories
486 such as “no habitat conversion” and “grassland to woody savannah”. We focused on the eight
487 most frequent types of habitat conversion (Extended Data Figure 7).
488
489 By synthesising information from scenario data based on Earth Dynamics Models (LUH) and
490 remote-sensing databases (GFC, MODIS), we were able to determine historic forest loss from
491 the start of the monitoring period to 2015, as well as contemporary forest cover change (gain
492 and loss) and habitat transitions from 2000 to 2016. GFC and MODIS detect forest cover, with
493 no distinction between primary and secondary forests, thus we derived information on
494 transitions from primary to secondary forest from the LUH database. We calculated overall
495 forest cover change because we considered total change in habitat to be more meaningful for
496 long-term population and biodiversity trends as opposed to an annual rate of forest cover

change which does not capture cumulative effects. Together, the three databases (GFC, MODIS, LUH) encompass two different elements of land-use change: 1) land cover types and long-term historical reconstructions of past land-use and habitat conversions and 2) high-resolution satellite data from recent years of forest cover change and habitat conversion types. Thus, the combined analysis allows for a comprehensive test of the effects of land-use change on populations and biodiversity around the world.

Population time series data (Living Planet Database)

We analysed 4,228 population time series, with records distributed around the world. Geographic representation is variable with, for example, an under-representation of tropical regions in the population data (Figure 1). In the LPD, some populations have precise coordinates, whereas the location of others are approximate. Because of the extent over which we are calculating forest cover change (96 km^2), we included both types of populations in our analysis. Duration varied across time series (Extended Data Figure 4c-d) and we only included populations with at least five survey points. The overall range of the time series covered the period between the years 1970 and 2014. We calculated population change using state-space models which are particularly appropriate when quantifying change in data with varying collection methodology, as they take into account observation error and process noise[50,51]. For more details on state-space model calculations, see Humbert *et al.* 2009[34] and Daskalova *et al.* 2018[1]. We scaled the population size data to be between 0 and 1 to analyse within-population relationships and to make sure that we were not conflating within-population relationships and between-population relationships[52]. State-space models partition the variance in abundance estimates into process error (σ^2) and observation or measurement error (τ^2) and estimate population trends (μ):

$$X_t = X_{t-1} + \mu + \varepsilon_t, (1)$$

522 where X_t and X_{t-1} are the scaled (observed) abundance estimates (between 0 and 1) in the

523 present and past year, with process noise represented by $\varepsilon_t \sim gaussian(0, \sigma^2)$. We included

524 measurement error following:

525 $$Y_t = X_t + F_t,$$

526 where Y_t is the estimate of the true (unobserved) population abundance with measurement

527 error:

528 $$F_t \sim gaussian(0, \tau^2).$$

529 We substituted the estimate of population abundance (Y_t) into equation 1:

530 $$Y_t = X_{t-1} + \mu + \varepsilon_t + F_t.$$

531 Given $X_{t-1} = Y_{t-1} - F_{t-1}$, then:

532 $$Y_t = Y_{t-1} + \mu + \varepsilon_t + F_t - F_{t-1}.$$

533

534 For each time series, we calculated overall population change (μ) experienced 1) across the

535 periods before and after contemporary peak forest loss, 2) across the full duration of the time

536 series, 3) from 2000 to 2016 (matching the temporal scale of the GFC database), and 4) from

537 2000 to 2013 (matching the temporal scale of the MODIS database). We standardised the

538 number of years over which we calculated population change before and after peak forest loss

539 on the population-level, meaning that the number of years before and after was the same within

540 populations, but might differ among populations.

541

542 *Biodiversity time series data (BioTIME Database)*

543 We analysed 2,339 time series from 190 studies from terrestrial biomes across the globe, part

544 of the BioTIME database[13] (with the addition of 36 studies that are not yet a part of the public

545 database). Similarly to the LPD, tropical regions and some taxa such as amphibians and reptiles

were under-represented. Some of the study locations fall within protected areas (32%). Because those studies only had one time series each, overall only 1% of analysed time series were from inside protected areas. To account for the different spatial extents of the BioTIME database and uneven sampling, studies with multiple locations and extents > 72 km^2 were partitioned into 96 km^2 grids, and then sample-based rarefaction was applied to standardise sampling within each time series[14]. Duration varied across time series (Extended Data Figure 4c-d) and the overall range of the time series covered the period between the years 1858 and 2016. For time series with five or more years of monitoring records, we calculated overall richness change and turnover experienced 1) across the periods before and after contemporary peak forest loss, 2) across the full duration of the time series. For time series with two or more years of monitoring records, we calculated overall richness change and turnover experienced 3) from 2000 to 2016 (matching the temporal scale of the GFC database), and 4) from 2000 to 2013 (matching the temporal scale of the MODIS database). The GFC and MODIS databases cover shorter time periods, thus we included biodiversity time series with shorter durations than the five-year cut off point that was used in the rest of our analyses using datasets with longer durations (but note that 76% of biodiversity time series had a duration of three or more years). To estimate richness change, we modelled species richness versus time (year, mean centered) with random slopes and intercepts for each rarefied cell and a Poisson error distribution with a log link.

$$log(\mu_{j,i,t}) = \beta_0 + \beta_{0j} + \beta_{0j,i} + (\beta_1 + \beta_{1j} + \beta_{1j,i})year_{j,i,t},$$

$$y_{j,i,t} \sim poisson(\mu_{j,i,t}),$$

where $year_{j,i,t}$ is the time in years, β_0 and β_1 are the global intercept and slope (fixed effects), β_{0j} and β_{1j} are the biome-level departures from β_0 and β_1 (respectively; biome-level random effects), $\beta_{0j,i}$ and $\beta_{1j,i}$ are the (nested) cell-level departures from β_0 and β_1 (cell-level random effects); $y_{j,i,t}$ is the (rarefied) species richness within the jth biome in the ith cell in year t.

570

571 From the richness over time model, we extracted the posterior means for richness change for
572 each time series (i.e., the cell-level slope estimates), which then became the response variable
573 in the second stage of our analyses where we tested richness change versus forest cover
574 change (see Statistical analyses section).

575

576 To determine changes in community composition, we calculated the turnover component of
577 beta diversity (changes due to species replacement rather than changes in species
578 abundances[14,35]), at the end of each time period outlined above relative to the first year of
579 observation in the same period. Turnover is bound between zero and one, where zero is no
580 change in species composition and one indicates that all of the original species of a community
581 have been replaced with new species.

582

583 **Statistical analyses**

584 When testing for an attribution signal (i.e., evidence that a predictor variable is a potential driver
585 of population or biodiversity change), we always matched the temporal scales of the forest cover
586 change data and the population and biodiversity data. For example, when testing the effects of
587 forest cover change and land-use transitions as detected by GFC (2000 – 2016) and MODIS
588 (2000 – 2013), we calculated population and biodiversity change for the same time periods.
589 Because of the longer duration of the LUH database, we were also able to extract forest and
590 land cover information for the full duration of the LPD and BioTIME time series. For our analyses
591 of contemporary peak forest loss and overall forest loss (using the LUH database over a time
592 period matching the duration of each time series), we excluded locations which had less than
593 0.05 (out of maximum 1) forest cover change. We excluded locations which had no forest cover
594 across the duration of the time series in both the 96 km^2 cells and the 500 km^2 larger landscape

cells from our analyses of population and biodiversity change versus forest cover gain and loss from 2000 to 2016 (using the GFC database). See Extended Data Table 1 for the outputs of all statistical models and their respective sample sizes.

Population and biodiversity change after versus before contemporary peak forest loss

To test if temporal population and biodiversity change differed before and after peak forest loss on the site-level, we split each time series into two periods – before and after peak deforestation – and estimated population change, richness change and turnover for each period separately. Then, to infer if population and biodiversity change differed following peak forest loss, we modelled μ (population change), richness change (cell-level random slopes) and turnover as a function of period (categorical with two levels – before or after forest loss) and time series duration (numeric) as fixed effects, with a biome random effect to account for the spatial clustering of the data. For population and richness change, we modelled the positive and negative components of the distributions of change separately, e.g., one model for populations with positive μ values and one model for populations with negative μ values. This approach allowed us to test if the effects of forest loss differ across the positive and negative dimensions of population and biodiversity change. The models were as follows:

$$\mu_{j,i,p} = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i,p} + \beta_2 * period_{j,i,p},$$

$$y_{j,i,p} \sim gaussian(\mu_{j,i,p}, \sigma^2),$$

where $duration_{j,i,p}$ is the duration of the time series in years of cell i within biome j for period p, and $period_{j,i,p}$ is an indicator variable for the period (before or after forest loss); β_0, β_1 and β_2 are the global intercept and slope estimates for duration and the categorical period effect, respectively (fixed effects), β_{0j} is the biome-level departures from β_0 (biome-level random

effects); $y_{j,i,p}$ is the estimate for change in population size or species richness for the ith cell in the jth biome for the pth period.

To model the change in turnover before and after contemporary peak forest loss, we followed the same conceptual framework as outlined above, but we used 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. In the parameterisation approach we used[53] ϕ is inversely related to the variance. Beta parameterisation is also sometimes expressed through the parameters p and q that can be derived from our framework following $\phi = p + q$[54]. Because only 7% of time series did not experience any change in species composition (y = 0) in the time period after contemporary forest loss, and less than 1% of time series had a completely new set of species (y = 1) occupying the ecological communities, for y = 0 and y = 1, α and γ were modelled assuming a Bernoulli distribution and logit-link function, and models were fit with only an intercept. For 0 < y < 1, we assumed a beta error distribution and a logit-link function:

$$logit(\mu_{j,i,p}) = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i,p} + \beta_2 * period_{j,i,p},$$

$$y_{j,i,p} \sim Beta(\mu_{j,i,p}, \phi),$$

where $duration_{j,i,p}$ is the duration of the time series in years of cell i within biome j for period p, and $period_{j,i,p}$ is an indicator variable for the period (before or after forest loss); β_0, β_1 and β_2

are the global intercept and slope estimates for duration and the categorical period variable respectively (fixed effects), and β_{0j} are the biome-level departures from β_0 (biome-level random intercepts); $y_{j,i,p}$ is the estimate of turnover for the ith cell in the jth biome for the pth period.

Population change before, after and during the period of all-time historic peak forest loss

To determine if population change differed based on whether population time series were recorded before, during, or after the period of all-time historic peak forest loss (the timing of the largest forest loss event at the location of each time series between the years 850 and 2015), we modelled μ (population change) as a function of when monitoring started (categorical with three levels – before, during or after peak forest loss) and time series duration (numeric) as fixed effects, with a biome random effect to account for the spatial clustering of the data. Low sample size precluded a similar analysis for biodiversity change (Extended Data Figure 3). The model was as follows:

$$\mu_{j,i,m} = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i,m} + \beta_2 * monitoring\ start_{j,i,m},$$

$$y_{j,i,m} \sim gaussian(\mu_{j,i,m}, \sigma^2),$$

where $duration_{j,i,m}$ is the duration of the time series in years of cell i within biome j for monitoring start m, and $monitoring\ start_{j,i,m}$ is an indicator variable denoting when monitioring started; β_0, β_1 and β_2 are the global intercept and slope estimates for duration and the categorical monitoring start variable respectively (fixed effects), β_{0j} is the biome-level departures from β_0 (respectively; biome-level random effects); $y_{j,i,m}$ is the estimate for change in population size or species richness for the ith cell in the jth biome for the mth monitoring start.

Habitat conversion and population and biodiversity change

To determine the influence of the type of forest cover change (i.e., land-use transitions) on population and biodiversity change, we compared the distributions of population and biodiversity change across transitions types (from primary forest to secondary forest, from primary forest to non-natural habitat, and from secondary forest to non-natural habitat, to which we refer as habitat conversion). Small sample sizes (on average 10 time series per transition type) precluded statistical analysis, thus we report findings from a visual inspection of distributions of population and biodiversity change across habitat conversion types.

To test the effect of forest cover change on population and biodiversity change among sites, we modelled population and biodiversity change versus overall forest cover change (calculated as forest cover gain and forest cover loss (GFC database, 2000-2016) and forest loss (LUH database, across the duration of the time series). Models of population and richness change versus forest cover change were fitted assuming Gaussian error.

$$\mu_{j,i} = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i} + \beta_2 * forest\ change_{j,i},$$

$$y_{j,i} \sim gaussian(\mu_{j,i}, \sigma^2),$$

where $duration_{j,i}$ is the duration of the time series in years of cell i within biome j, $forest\ change_{j,i}$ is the forest cover change in cell i within biome j; β_0, β_1 and β_2 are the global intercept and slope estimates for duration and forest cover change respectively (fixed effects), and β_{0j} are the biome-level departures from β_0 (biome-level random intercepts); $y_{j,i}$ is the population or richness change metric (a separate model for population declines, population increases, richness losses and richness gains) in the ith cell within the jth biome.

Models of turnover versus forest cover change were fit with a zero one inflated beta distribution to account for the properties of turnover (bounded between zero and one). We used the same

probability density function for the zero one inflated beta distribution as in the model for turnover before and after contemporary peak forest loss. For y = 0 and y = 1, α and γ were modelled assuming a Bernoulli distribution and logit-link function, and we fit models with only an intercept. For 0 < y < 1, we assumed a beta error distribution and a logit-link function:

$$logit(\mu_{j,i}) = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i} + \beta_2 * forest\ change_{j,i},$$

$$y_{j,i} \sim Beta(\mu_{j,i}, \phi),$$

where duration$_{j,i}$ is the duration of the time series in years of cell i within biome j, $forest\ change_{j,i}$ is the forest cover change in cell i within biome j; β_0, β_1 and β_2 are the global intercept and slope estimates for duration and forest cover change respectively (fixed effects), and β_{0j} are the biome-level departures from β_0 (biome-level random intercepts); $y_{j,i}$ is turnover in the ith cell within the jth biome.

Lags in population and biodiversity responses to contemporary peak forest loss

To test for temporal lags in population and biodiversity responses to contemporary peak forest loss, we first calculated when population and biodiversity change were greatest following peak forest loss for each time series. Rates of population change were calculated using state-space models and a Kalman filter[20,34]. Peak richness change and peak turnover were calculated as the maximum value of the absolute differences between consecutive observations of species richness and turnover. We then quantified lag as the number of years between contemporary peak forest loss and peak population/biodiversity change. We modelled lag as a function of taxa, as we expect that species with longer generation times will respond to disturbance more slowly.

$$\mu_{j,i} = \beta_{0j} + \beta_1 * taxa_{j,i},$$

$$y_{j,i} \sim gaussian(\mu_{j,i}, \sigma^2),$$

where $taxa_{j,i}$ is the taxa of the cell i in the biome j time series, β_1 is the slope for taxa effect (fixed effect), and β_{0j} are the biome-level random intercepts; $y_{j,i}$ is the temporal lag in the population or biodiversity change metric (a separate model for population change, richness change and turnover) for the ith cell within the jth biome.

We conducted a *post-hoc* analysis where we tested our temporal lag and generation time hypothesis in a more quantitative manner by modelling lag as a function of generation time in mammals, the taxa for which generation time data were freely available[55].

$$\mu_g = \beta_0 + \beta_1 * generation\ time_g,$$

$$y_g \sim gaussian(\mu_g, \sigma^2),$$

where $generation\ time_g$ is the mammal generation time in years, β_0 and β_1 are the global intercept and slope (fixed effect); y_g is the temporal lag in population change for a species with generation time g.

Prior specification

For all models except the model of turnover versus overall forest cover change (which was a zero one inflated model), we used 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 that had a zero one inflated beta distribution, we used 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 rarefied cell random effect in the species richness over time model, i, and the biome random effect in all models, j) were all assumed to be $gaussian(0, \sigma)$, and priors on the σ were the same for all models:

$$\sigma\beta_{0j} = \sigma\beta_{0j,i} \sim half\ Cauchy(0, 2).$$

All models were fitted in a Bayesian framework using the *brms* package v2.1.0[53] in R v3.5.1[56]. Models were run for 6000 iterations, with a warm up of 2000 iterations. Convergence was assessed 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).

Sensitivity analyses

Our analyses were not sensitive to our calculation of turnover in the final year of the time series relative to the first year, and previous examinations of the BioTIME database have found that calculating turnover relative to the second year of observation produced similar results[4]. We also quantified population change using the BioTIME database (following the same state-space modelling framework as with the LPD) and found similar lack of directional patterns in the relationships between population change and overall forest loss (Extended Data Figure 5f). We found no distinct geographic or taxonomic patterning in the relationships between population change, biodiversity change and forest cover change (Extended Data Figure 9). Furthermore, the relationships between population decreases and increases and forest loss were not influenced by whether species were tightly associated with forests or not (Extended Data Figure

5g-i). Similar *post-hoc* analysis was not possible for the biodiversity time series because habitat preference data were not available for many of the species included in the BioTIME database. The cell size over which we calculated forest cover change (from 10 km^2 to 500 km^2) did not influence overall findings, as detected forest cover change scaled proportionately with cell size across locations (Extended Data Figure 10a-b). Landscape context (forest cover in a 500 km^2 cell around sites) also did not influence the relationship between forest cover change and population and biodiversity change (Extended Data Figure 10c-d). We did not find directional patterns between population and biodiversity change and time since the largest forest loss event (Extended Data Figure 10f-h). Our findings were not influenced by the type of forest cover (primary vs secondary), as loss of secondary forest cover scaled proportionately to primary forest loss (Extended Data Figure 10e).

Supplementary methods references

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Data and code availability

Code for the rarefaction of the BioTIME Database is available from https://doi.org/10.5281/zenodo.1475218. Code for statistical analyses is available from http://doi.org/10.5281/zenodo.1490144. Population and biodiversity data are freely available in the Living Planet and BioTIME Databases[12,13]. 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/). Land-use change data are publicly available in the Land Use Harmonization Database[30], the Forest Cover Change Database[31], and the MODIS Landcover Database[32].