

1 **Forest loss as a catalyst of population and biodiversity change**

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26 Extended Data Figures: 10

27 Extended Data Tables: 1

28 **Summary**

29 Accelerating human impacts are reshaping Earth's ecosystems. Populations¹, richness²⁻⁴ and
30 composition⁴ of communities at sites around the world are being altered over time in complex
31 and heterogeneous ways⁵⁻⁷. Land-use change is thought to be the greatest driver of this
32 population and biodiversity change in terrestrial ecosystems⁸⁻¹⁰. However, a major knowledge
33 gap is whether land-use change drivers, such as forest loss and habitat conversion, can indeed
34 explain the high heterogeneity of temporal population and biodiversity trends^{9,11}. Here, we fill
35 this gap by analysing change in 6,667 time series of populations (species' abundance)¹² and
36 biodiversity (species richness and turnover in ecological communities)¹³ over one and a half
37 centuries of forest cover change and habitat transitions. We revealed an acceleration in both
38 increases and decreases in population size, species richness and turnover after peak forest
39 loss at over 2,000 sites across the globe. We found that temporal lags in population and
40 biodiversity change following forest loss can extend up to half of a century and were longer for
41 species with longer generation times such as large mammals. Together, our results
42 demonstrate that historic and contemporary forest cover change do not universally lead to
43 population declines and biodiversity loss, though population declines were most pronounced
44 during and immediately following peak forest loss. By explicitly quantifying multi-decadal
45 temporal lags in population and biodiversity responses to land-use change, our findings inform
46 projections of how life on Earth will be reshaped across the Anthropocene.

47

48 **Main text**

49 Earth's biodiversity is changing^{3-5,14}. At sites across the planet, populations are increasing and
50 decreasing^{1,15,16}, species are lost¹⁷ and gained^{18,19}, yet synthesis studies across sites indicate
51 no net change in local scale species richness^{3,4} despite marked shifts in species composition
52 (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-regulation²⁷. Such temporal
59 discrepancies in the magnitude of effects have been observed when studying the impacts of
60 warming on community change²⁵, and of habitat fragmentation on populations and
61 biodiversity^{28,29}. The integration of multi-century long reconstructions of past land cover³⁰ 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.

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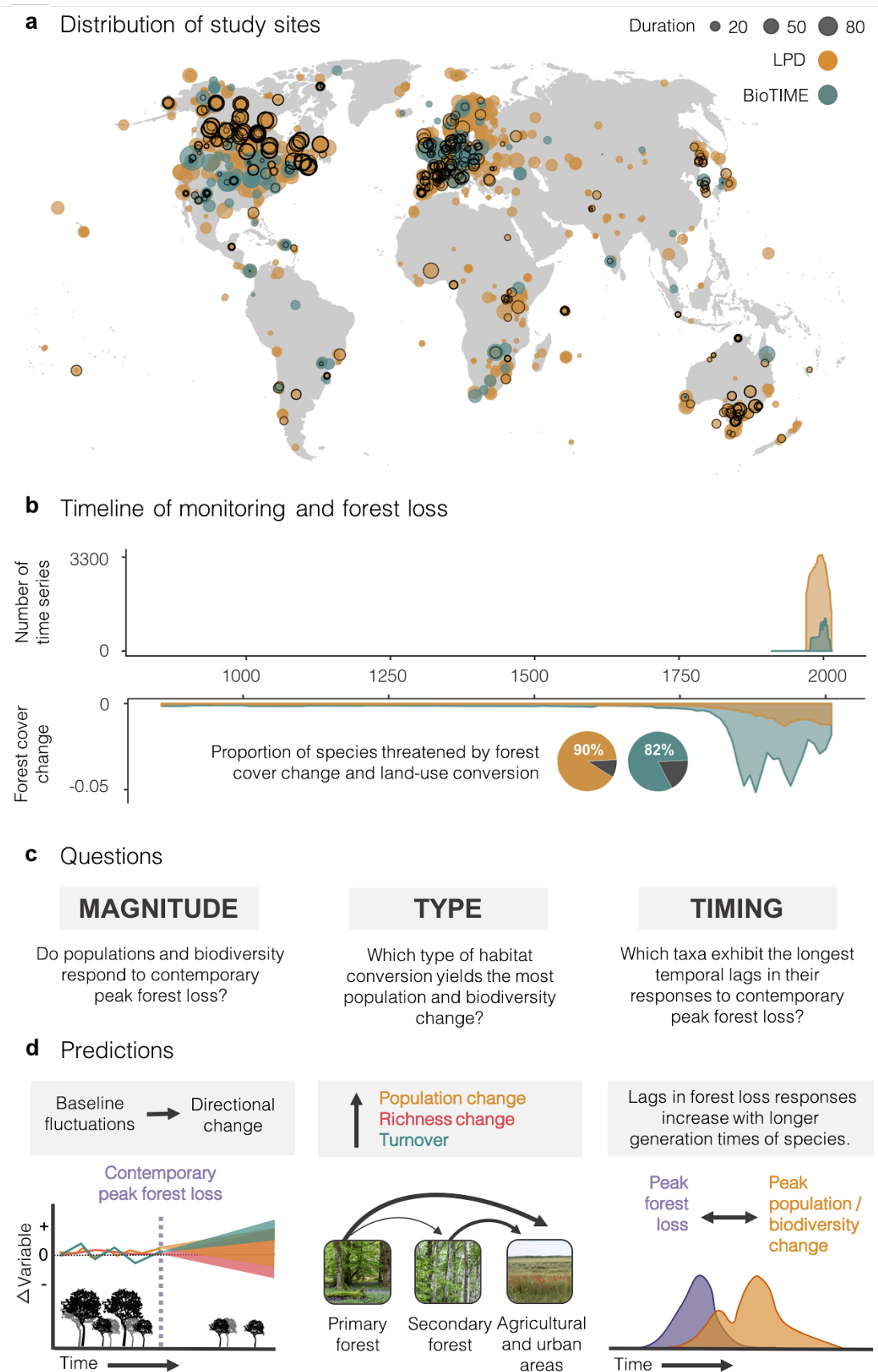
68 Here, we asked how populations (trends in numerical abundance) and biodiversity (trends in
69 species richness and community composition) across vertebrate, invertebrate and plant taxa
70 vary according to the timing and magnitude of forest cover change and habitat conversions
71 (Figure 1, Extended 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 biomes³³ 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 fluctuations³⁴.
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 turnover³⁵ 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 species³⁷ (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

103 conditions prompting local extinctions but also colonisations by new species^{27,36}. Secondly, we
104 predicted that the largest population declines will occur during the periods of all-time peak forest
105 loss across sites as that is the baseline for maximum intensity of forest cover change²⁶. Finally,
106 we predicted that temporal lags will be greater for species with longer generation times, as they
107 typically respond more slowly to environmental change⁴⁰ and have more limited dispersal⁴¹. If
108 we find support for our overall prediction that population and biodiversity loss will be greater
109 with higher forest loss, this would indicate that forest loss is a key driver of rapid and pervasive
110 declines over time. Alternatively, if we find support for heterogeneous and temporally-delayed
111 responses of populations and ecological communities to forest loss, this would imply that the
112 effects of land-use change over time are more complex than previously thought, which has
113 implications for improved prediction of future ecological change and development of biodiversity
114 and conservation policy.

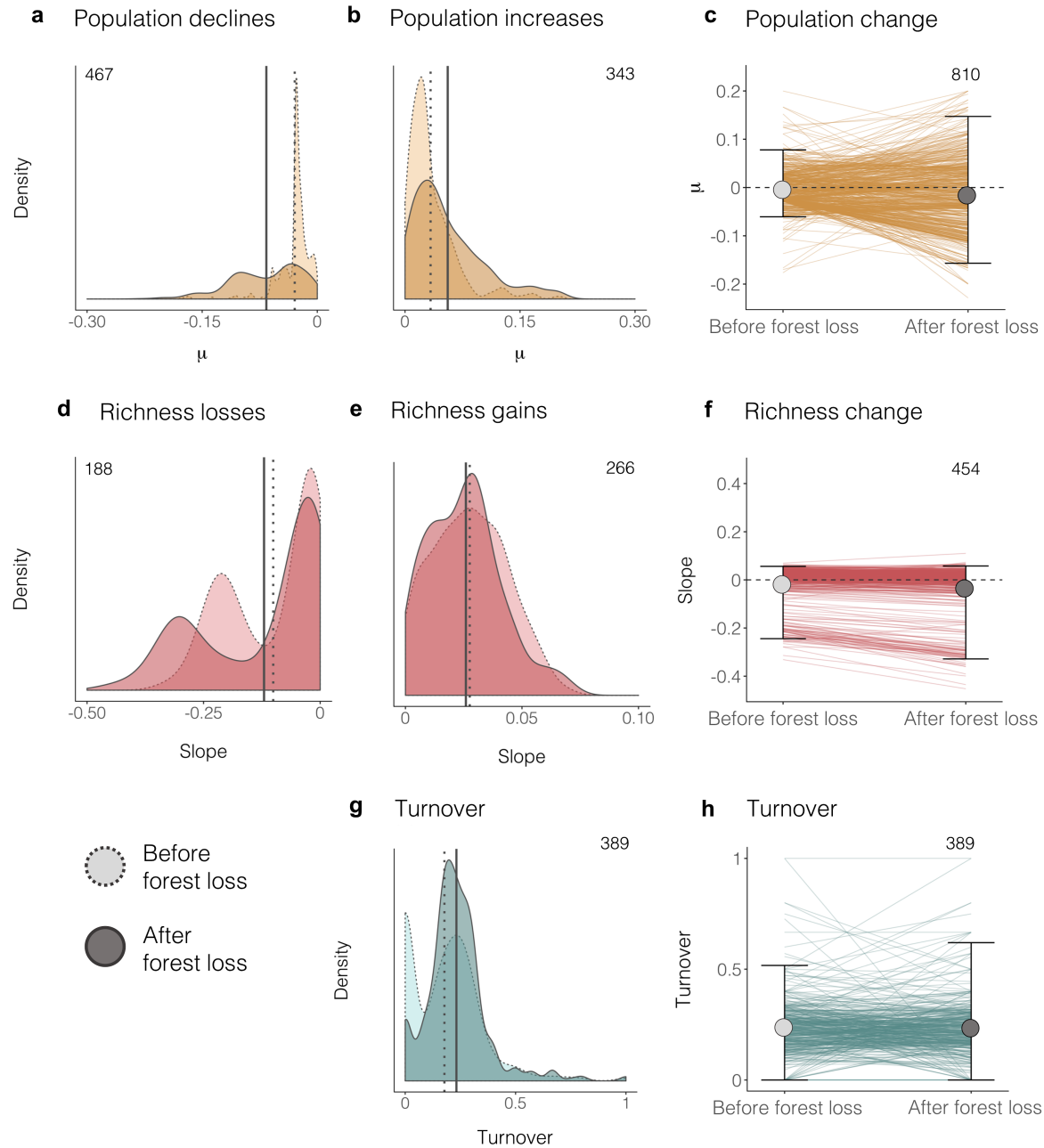


116 **Figure 1. Forest cover change can influence population and biodiversity change through**
117 **multiple mechanisms.** For 38% of population time series and 70% of biodiversity time series
118 monitoring began after historic peak forest loss had already occurred (see Extended Data
119 Figures 2-3, 4a-b). See Extended Data Figure 1 for workflow of analyses. **a**, Global map of
120 locations and duration of 542 Living Planet Database (LPD) and 190 BioTIME studies,
121 containing the 6,497 time series from 2,154 locations analysed here. From the total number of
122 time series analysed, 2,852 had experienced historic or contemporary forest cover gains and
123 losses. Black outlines on **a** indicate locations that were forested at the start of the population
124 or biodiversity monitoring period (1,247 sites). **b**, Timeline of monitoring and forest loss across
125 the LPD and BioTIME databases (for variation in monitoring duration among time series, see
126 Extended Data Figures 2-4). Forest loss was quantified over 10-year periods across 96 km²
127 cells as a proportion, with e.g., -0.05 meaning a 5% loss of forest cover. Inset on **b** shows the
128 proportion of species, part of the LPD and BioTIME databases, that are threatened by land-use
129 change, based on species' IUCN threat assessments (see Extended Data Figure 4e). **c-d**,
130 Questions and predictions for this study outlined with respect to population change, richness
131 change and turnover (species composition change). Habitat conversion refers to a change in
132 the dominant land cover type. Photos in **d** are by G. N. Daskalova.

133

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

141 -0.03, Figure 2a). Similarly, 66% of the increasing populations experienced even more positive
142 population change after peak forest loss (slope = 0.02, CI = 0.02 to 0.03, Figure 2b). In contrast,
143 among time series, we did not find directional relationships among greater forest loss and
144 population and species richness declines (Figure 3, Extended Data Figures 5-7). This
145 disconnect between the magnitude of land-use change and population and biodiversity change
146 could be due to a number of factors including temporal lags in population or community
147 responses^{26,40} and/or less forest cover change having occurred during the monitoring period
148 relative to historic forest clearing^{26,42,43} (Extended Data Figures 2-3). In further contrast to our
149 first prediction, larger magnitudes of forest loss often led to greater increases, rather than
150 decreases, in species richness over time, particularly among time series comparisons with
151 shorter durations (Extended Data Figure 6e). Forest loss is a key driver of habitat fragmentation
152 which can lead to rapid colonisation by new species due to increased landscape heterogeneity
153 and larger breadth of ecological niches across sites^{5,28,36}. Our results highlight that the same
154 global change driver, forest loss, affects populations and ecological communities in
155 heterogeneous ways at different sites around the world, and accounting for this heterogeneity
156 is key when scaling from local impacts of human activities to global scale biodiversity patterns
157 and attribution of change¹⁰.



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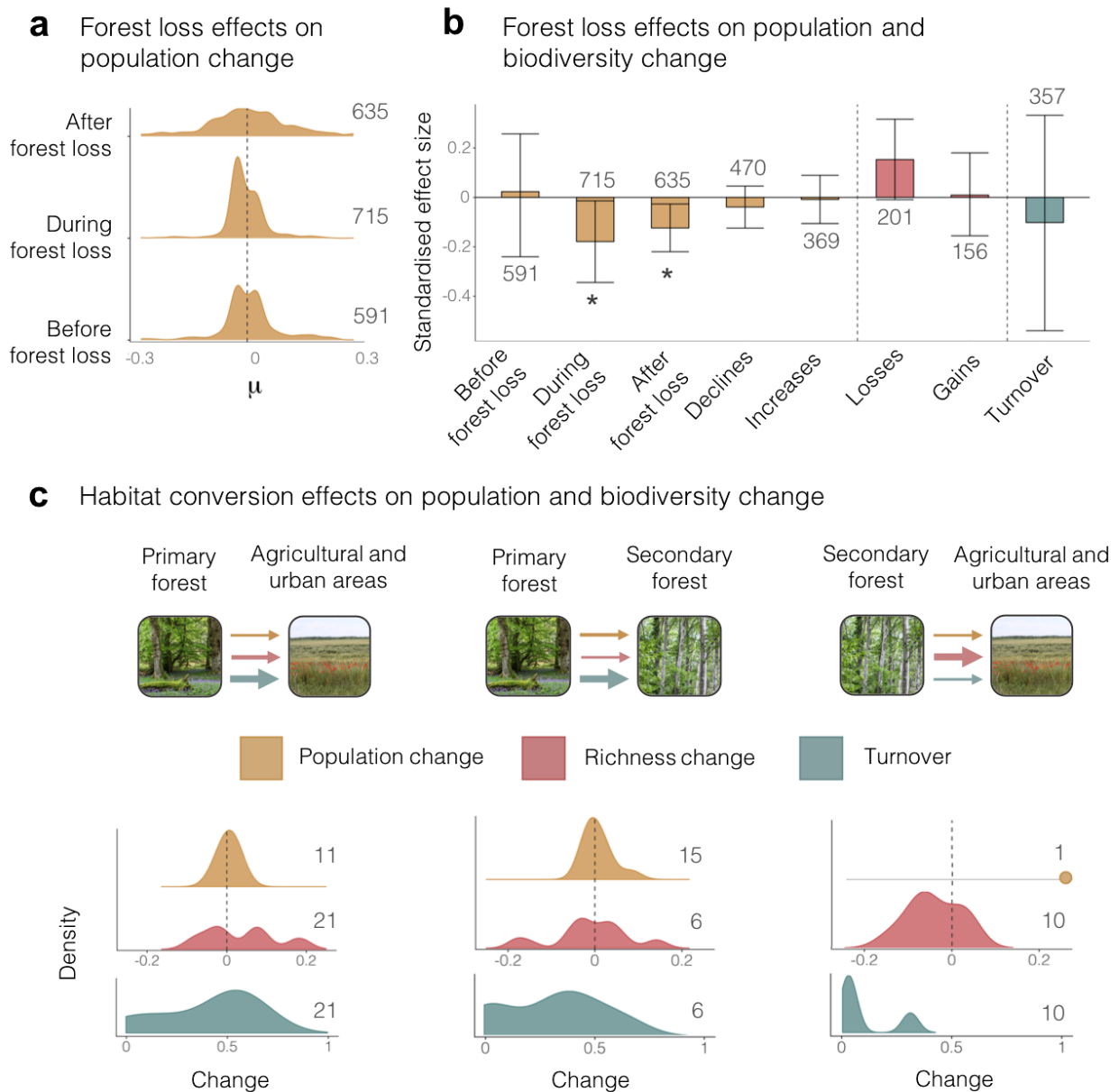
159 **Figure 2. At the site level, population and biodiversity change increase after**
 160 **contemporary peak forest loss.** Though species richness tended to decrease after peak forest
 161 loss, the proportion of populations that experienced increases and declines in population
 162 abundance and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

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

176

177 Our results revealed that population declines were most pronounced during the period of all-
178 time peak forest loss and turnover was highest when primary forests were converted to
179 agricultural and urban areas (Figure 3). Following peak contemporary forest loss, turnover
180 increased by over 10% in 19% of the time series (Figure 2), further testifying to the high rates
181 of compositional change detected across the Anthropocene^{4,5,14}. However, within 22% of the
182 time series, turnover declined by over 10% after forest loss, suggesting that biotic
183 homogenisation might also be occurring following human-induced environmental change⁴⁴.
184 Taken together, our findings suggest site-specific impacts that were stronger and more common
185 when the population and biodiversity monitoring captured the largest forest loss events and the
186 most dramatic habitat conversion events across time relative to when monitoring is mismatched
187 with forest cover change (Figures 2-3). A greater proportion of the planet is projected to
188 experience an unprecedented amount of land-use change in the coming decades⁴⁵, highlighting

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



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192 **Figure 3. Population declines were most acute when the all-time peak in deforestation**

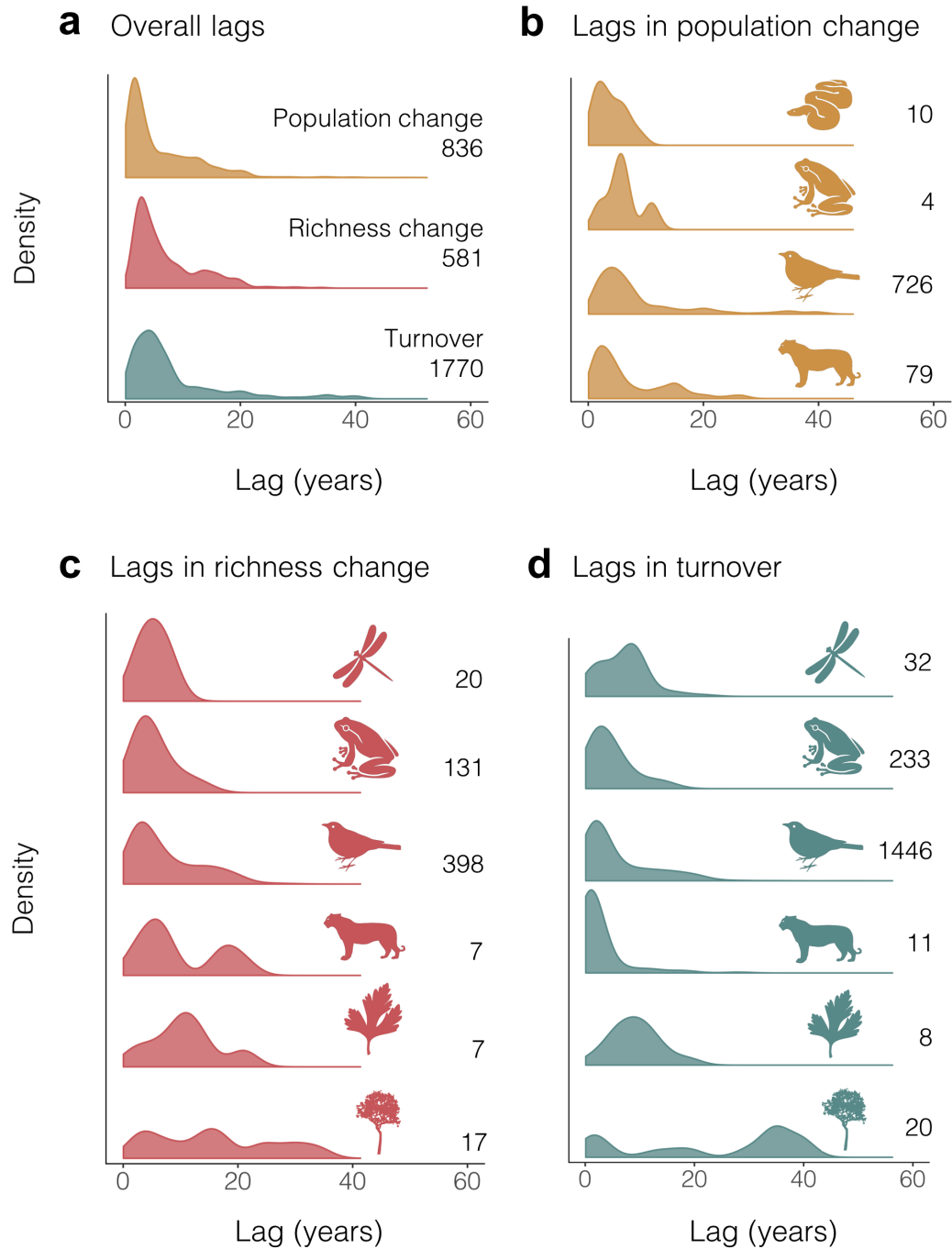
193 **for study sites occurred within the duration of population monitoring. a, Population**

194 declines are more likely to be detected when peak deforestation occurs during the population

195 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 database¹², 2000-2016) and forest cover loss (LUH database¹¹, 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 Database³².
219

220 We found evidence for up to half-century ecological lags in changes in population abundance,
221 species richness and community composition following forest loss (Figure 4). On average, we
222 documented maximum change in populations and biodiversity six to 13 years after
223 contemporary peak forest loss across taxa. Yet, nearly half of population and biodiversity
224 change (40%) occurred within three years of peak forest loss, demonstrating that rapid shifts in
225 populations and ecological communities occur frequently (Figure 4a). As predicted, the period
226 between peak forest loss and peak change in populations and biodiversity was longer for taxa
227 with longer generation times (e.g., large mammals, Figure 4b, Extended Data Table 1), further
228 confirmed by a *post-hoc* analysis of lags in population change versus mammal generation time
229 (Extended Data Figure 8a). Population declines and increases occurred on similar time scales
230 (Extended Data Figure 8b-c), potentially explaining why previous temporal analyses of
231 population change have not found evidence for net population declines^{1,20}. Losses in species
232 richness lagged behind richness gains only by approximately half a year (slope = 0.5, CI = 0.1
233 – 1.05), indicating that potential extinction debts and immigration credits accumulated at roughly
234 the same speed across taxa. The similar pace and temporal delay of richness gains and losses
235 could be the source of the previously observed findings of no net local richness change^{3,4}, yet
236 substantial compositional change^{2,4} across sites and taxa. Such temporal lags in biodiversity
237 change have also been observed in post-agricultural forests^{2,46} and fragmented grasslands⁴⁰,
238 where agricultural activity has ceased decades to centuries ago, yet richness and community
239 composition change continue to the modern-day. Overall, our results indicate that increasing
240 rates of land-use change in the Anthropocene^{11,45} will alter ecosystems on both short- and long-
241 term timescales.



242

243 **Figure 4. Population and community change after peak forest loss may be delayed by up**

244 **to half a century across 3,187 time series from around the world, with species with long**

245 **generation times and low mobility showing the largest temporal lags. a, Distributions of**

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

255

256 In summary, our analysis reveals an acceleration of increases and decreases of populations
257 and biodiversity after forest loss and habitat conversion at sites around the planet. Our findings
258 that all is not loss contrast with our hypothesis and challenge the widely-held assumption that
259 land-use change universally leads to population declines and species richness loss^{8,15,23}.
260 Nevertheless, the increased magnitude and likelihood of population declines during and
261 following peak forest loss highlight that human impacts are altering the biodiversity of the planet
262 and emphasize the importance of expanded biodiversity monitoring in current and future
263 hotspots of land-use change. A critical assumption underlying existing projections of biodiversity
264 responses to land-use change^{8,23} is that space-for-time approaches accurately reflect longer-
265 term population and biodiversity dynamics¹¹. On the contrary, we find that temporal lags in
266 population and biodiversity change following forest loss varied by taxa and generation time and
267 extended up to half of a century. Over the Anthropocene, ecosystems could be responding to a
268 suite of global change drivers, in addition to land-use change, and a key next research step is
269 to test the synergy and discord between the effects of multiple anthropogenic threats on Earth's
270 biota. Our results highlight the complex biological responses to habitat conversion across sites,

271 taxa and time scales that are leading to the reorganisation of ecological communities. Thus,
272 indicators used to assess biodiversity change regionally and globally¹⁰, including progress
273 towards Aichi targets⁴⁷, must capture the full spectrum and temporal spread of population and
274 biodiversity responses to human impacts across the Anthropocene.

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388

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403

404 **Author contributions**

405 G.N.D., M.A.D. and I.M.S. conceptualised the study. G.N.D. integrated databases and
406 conducted statistical analyses with input from S.B., I.M.S., A.D.B. and M.A.D. G.N.D. created
407 the figures with input from co-authors. S.B. and S.S. wrote the code for the rarefaction of the
408 BioTIME studies. I.M.S. was the primary supervisor and M.A.D. the co-supervisor for G.N.D.
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410 and all authors contributed to revisions.

411

412 **Methods**

413 For an illustration of the workflow of our analyses of forest cover and population and biodiversity
414 change through time, see Extended Data Figures 1 and 3b. All data and statistical analyses are
415 described in detail below. We did not predetermine sample size and instead worked with all
416 available temporal population, biodiversity and forest cover change data that met our duration
417 criteria. For analyses of population change, we included time series with five or more survey
418 points. For analyses of biodiversity change, we included time series with five or more data points
419 when analysing the full time series, and time series with two or more data points when matching
420 the duration of time series comparisons to the 16-year duration of the Global Forest Change
421 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 km² cells around the location of each population in the
435 LPD database and for the standardised grid cells of the BioTIME database (~ 96 km² 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 km² cells
462 around the location of each population in the LPD database and for the standardised grid cells
463 of the BioTIME database (~ 96 km² each) from the Global Forest Change (GFC)³¹ database
464 using the Google Earth Engine⁴⁸. 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 km²) for each 96
467 km² 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 km² 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 wildfires⁴⁹. 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 Database³² 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

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

503

504 *Population time series data (Living Planet Database)*

505 We analysed 4,228 population time series, with records distributed around the world.
506 Geographic representation is variable with, for example, an under-representation of tropical
507 regions in the population data (Figure 1). In the LPD, some populations have precise
508 coordinates, whereas the location of others are approximate. Because of the extent over which
509 we are calculating forest cover change (96 km²), we included both types of populations in our
510 analysis. Duration varied across time series (Extended Data Figure 4c-d) and we only included
511 populations with at least five survey points. The overall range of the time series covered the
512 period between the years 1970 and 2014. We calculated population change using state-space
513 models which are particularly appropriate when quantifying change in data with varying
514 collection methodology, as they take into account observation error and process noise^{50,51}. For
515 more details on state-space model calculations, see Humbert *et al.* 2009³⁴ and Daskalova *et al.*
516 2018¹. We scaled the population size data to be between 0 and 1 to analyse within-population
517 relationships and to make sure that we were not conflating within-population relationships and
518 between-population relationships⁵². State-space models partition the variance in abundance
519 estimates into process error (σ^2) and observation or measurement error (τ^2) and estimate
520 population trends (μ):

521

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

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 $\varepsilon_t \sim \text{gaussian}(0, \sigma^2)$. We included
524 measurement error following:

$$525 \quad Y_t = X_t + F_t,$$

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

$$528 \quad F_t \sim \text{gaussian}(0, \tau^2).$$

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

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

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

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

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 database¹³ (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

546 were under-represented. Some of the study locations fall within protected areas (32%). Because
547 those studies only had one time series each, overall only 1% of analysed time series were from
548 inside protected areas. To account for the different spatial extents of the BioTIME database and
549 uneven sampling, studies with multiple locations and extents > 72 km² were partitioned into 96
550 km² grids, and then sample-based rarefaction was applied to standardise sampling within each
551 time series¹⁴. Duration varied across time series (Extended Data Figure 4c-d) and the overall
552 range of the time series covered the period between the years 1858 and 2016. For time series
553 with five or more years of monitoring records, we calculated overall richness change and
554 turnover experienced 1) across the periods before and after contemporary peak forest loss, 2)
555 across the full duration of the time series. For time series with two or more years of monitoring
556 records, we calculated overall richness change and turnover experienced 3) from 2000 to 2016
557 (matching the temporal scale of the GFC database), and 4) from 2000 to 2013 (matching the
558 temporal scale of the MODIS database). The GFC and MODIS databases cover shorter time
559 periods, thus we included biodiversity time series with shorter durations than the five-year cut
560 off point that was used in the rest of our analyses using datasets with longer durations (but note
561 that 76% of biodiversity time series had a duration of three or more years). To estimate richness
562 change, we modelled species richness versus time (year, mean centered) with random slopes
563 and intercepts for each rarefied cell and a Poisson error distribution with a log link.

$$564 \quad \log(\mu_{j,i,t}) = \beta_0 + \beta_{0j} + \beta_{0j,i} + (\beta_1 + \beta_{1j} + \beta_{1j,i})year_{j,i,t},$$

$$565 \quad y_{j,i,t} \sim \text{poisson}(\mu_{j,i,t}),$$

566 where $year_{j,i,t}$ is the time in years, β_0 and β_1 are the global intercept and slope (fixed effects),
567 β_{0j} and β_{1j} are the biome-level departures from β_0 and β_1 (respectively; biome-level random
568 effects), $\beta_{0j,i}$ and $\beta_{1j,i}$ are the (nested) cell-level departures from β_0 and β_1 (cell-level random
569 effects); $y_{j,i,t}$ is the (rarefied) species richness within the j th biome in the i th 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 km² cells and the 500 km² larger landscape

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

598

599 *Population and biodiversity change after versus before contemporary peak forest loss*

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

612
$$\mu_{j,i,p} = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i,p} + \beta_2 * period_{j,i,p},$$

613
$$y_{j,i,p} \sim gaussian(\mu_{j,i,p}, \sigma^2),$$

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

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

620

621 To model the change in turnover before and after contemporary peak forest loss, we followed
622 the same conceptual framework as outlined above, but we used a zero one inflated beta
623 distribution to account for the properties of turnover (bounded between zero and one, inclusive,
624 where one is a complete change in species composition). The probability density function for
625 the zero one inflated beta distribution is:

$$626 \quad \text{betainf}(y; \alpha, \gamma, \mu, \phi) = \begin{cases} \alpha(1 - \gamma), & y = 0 \\ \alpha\gamma, & y = 1 \\ (1 - \alpha)\gamma f(y; \mu, \phi), & 0 < y < 1, \end{cases}$$

627 where α is the probability that a zero or one occurs, γ is the probability that a one occurs (given
628 an observation is a zero or a one), and μ and ϕ are the mean and precision of the beta
629 distribution, respectively. In the parameterisation approach we used⁵³ ϕ is inversely related to
630 the variance. Beta parameterisation is also sometimes expressed through the parameters p and
631 q that can be derived from our framework following $\phi = p + q$ ⁵⁴. Because only 7% of time series
632 did not experience any change in species composition ($y = 0$) in the time period after
633 contemporary forest loss, and less than 1% of time series had a completely new set of species
634 ($y = 1$) occupying the ecological communities, for $y = 0$ and $y = 1$, α and γ were modelled
635 assuming a Bernoulli distribution and logit-link function, and models were fit with only an
636 intercept. For $0 < y < 1$, we assumed a beta error distribution and a logit-link function:

$$637 \quad \text{logit}(\mu_{j,i,p}) = \beta_0 + \beta_{0j} + \beta_1 * \text{duration}_{j,i,p} + \beta_2 * \text{period}_{j,i,p},$$

$$638 \quad y_{j,i,p} \sim \text{Beta}(\mu_{j,i,p}, \phi),$$

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

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

644

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

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

$$654 \quad \mu_{j,i,m} = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i,m} + \beta_2 * monitoring\ start_{j,i,m}$$

$$655 \quad y_{j,i,m} \sim gaussian(\mu_{j,i,m}, \sigma^2),$$

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

662

663 *Habitat conversion and population and biodiversity change*

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

671

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

$$677 \quad \mu_{j,i} = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i} + \beta_2 * forest\ change_{j,i},$$

$$678 \quad y_{j,i} \sim gaussian(\mu_{j,i}, \sigma^2),$$

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

685

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

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

$$692 \quad \text{logit}(\mu_{j,i}) = \beta_0 + \beta_{0j} + \beta_1 * \text{duration}_{j,i} + \beta_2 * \text{forest change}_{j,i},$$

$$693 \quad y_{j,i} \sim \text{Beta}(\mu_{j,i}, \phi),$$

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

699

700 *Lags in population and biodiversity responses to contemporary peak forest loss*

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

$$710 \quad \mu_{j,i} = \beta_0 + \beta_1 * \text{taxa}_{j,i},$$

$$711 \quad y_{j,i} \sim \text{gaussian}(\mu_{j,i}, \sigma^2),$$

712 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
713 (fixed effect), and β_{0j} are the biome-level random intercepts; $y_{j,i}$ is the temporal lag in the
714 population or biodiversity change metric (a separate model for population change, richness
715 change and turnover) for the i th cell within the j th biome.

716

717 We conducted a *post-hoc* analysis where we tested our temporal lag and generation time
718 hypothesis in a more quantitative manner by modelling lag as a function of generation time in
719 mammals, the taxa for which generation time data were freely available⁵⁵.

720

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

721

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

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

725

726 *Prior specification*

727 For all models except the model of turnover versus overall forest cover change (which was a
728 zero one inflated model), we used weakly regularising normally-distributed priors for the global
729 intercept and slope:

730

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

731

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

732 For the turnover models that had a zero one inflated beta distribution, we used the following
733 priors:

734

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

735

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

736 $zoi \sim \text{gaussian}(0, 0.5),$

737 $coi \sim \text{gaussian}(0, 0.5),$

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

740

741 Group-level parameters (the rarefied cell random effect in the species richness over time model,
742 i , and the biome random effect in all models, j) were all assumed to be $\text{gaussian}(0, \sigma)$, and priors
743 on the σ were the same for all models:

744 $\sigma\beta_{0j} = \sigma\beta_{0j,i} \sim \text{half Cauchy}(0, 2).$

745 All models were fitted in a Bayesian framework using the *brms* package v2.1.0⁵³ in R v3.5.1⁵⁶.

746 Models were run for 6000 iterations, with a warm up of 2000 iterations. Convergence was
747 assessed visually by examining trace plots and using *Rhat* values (the ratio of the effective
748 sample size to the overall number of iterations, with values close to one indicating convergence).

749

750 *Sensitivity analyses*

751 Our analyses were not sensitive to our calculation of turnover in the final year of the time series
752 relative to the first year, and previous examinations of the BioTIME database have found that
753 calculating turnover relative to the second year of observation produced similar results⁴. We
754 also quantified population change using the BioTIME database (following the same state-space
755 modelling framework as with the LPD) and found similar lack of directional patterns in the
756 relationships between population change and overall forest loss (Extended Data Figure 5f). We
757 found no distinct geographic or taxonomic patterning in the relationships between population
758 change, biodiversity change and forest cover change (Extended Data Figure 9). Furthermore,
759 the relationships between population decreases and increases and forest loss were not
760 influenced by whether species were tightly associated with forests or not (Extended Data Figure

761 5g-i). Similar *post-hoc* analysis was not possible for the biodiversity time series because habitat
762 preference data were not available for many of the species included in the BioTIME database.
763 The cell size over which we calculated forest cover change (from 10 km² to 500 km²) did not
764 influence overall findings, as detected forest cover change scaled proportionately with cell size
765 across locations (Extended Data Figure 10a-b). Landscape context (forest cover in a 500 km²
766 cell around sites) also did not influence the relationship between forest cover change and
767 population and biodiversity change (Extended Data Figure 10c-d). We did not find directional
768 patterns between population and biodiversity change and time since the largest forest loss event
769 (Extended Data Figure 10f-h). Our findings were not influenced by the type of forest cover
770 (primary vs secondary), as loss of secondary forest cover scaled proportionately to primary
771 forest loss (Extended Data Figure 10e).

772

773 **Supplementary methods references**

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793

794 **Data and code availability**

795 Code for the rarefaction of the BioTIME Database is available from
796 <https://doi.org/10.5281/zenodo.1475218>. Code for statistical analyses is available from
797 <http://doi.org/10.5281/zenodo.1490144>. Population and biodiversity data are freely available in
798 the Living Planet and BioTIME Databases^{12,13}. The Living Planet Database can be accessed on
799 http://www.livingplanetindex.org/data_portal. The BioTIME Database can be accessed on
800 Zenodo (<https://doi.org/10.5281/zenodo.1211105>) or through the BioTIME website
801 (<http://biotime.st-andrews.ac.uk/>). Land-use change data are publicly available in the Land Use
802 Harmonization Database³⁰, the Forest Cover Change Database³¹, and the MODIS Landcover
803 Database³².