Landscape-scale forest loss as a catalyst of population and biodiversity change

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Title: Landscape-scale forest loss as a catalyst of population and biodiversity change

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Abstract:

Global biodiversity assessments have highlighted land-use change as a key driver of biodiversity change. However, empirical evidence is lacking of how habitat transformations like forest loss and gain are reshaping biodiversity over time. Here, we quantify how change in forest cover has influenced temporal shifts in populations and ecological assemblages from 6,090 globally-distributed time series across six taxonomic groups. We found that local-scale increases and decreases in abundance, species richness, and temporal species replacement (turnover) were intensified by up to 48% following forest loss. Temporal lags in population- and assemblage-level shifts after forest loss extended up to 50 years and increased with species' generation time. Our findings show that land-use change catalyzes population and biodiversity change, emphasizing the complex biotic consequences of land-use change.

One Sentence Summary: Declines in forest cover amplify both gains and losses in population abundance and biodiversity over time.

Main Text:

Accelerating human impacts are reshaping Earth's ecosystems (*1*). The abundance of species' populations (*2*, *3*) and the richness (*4*–*6*) and composition (*6*) of ecological assemblages at sites around the world are being altered over time in complex ways (*6*–*8*, Fig. 3A). However, there is currently only a limited quantitative understanding of how global change drivers, such as land-use change, influence the observed heterogeneous local-scale patterns in population abundance and biodiversity (*8*, *10*, *11*). In terrestrial ecosystems, much current knowledge stems from space-for-time approaches (*12*, *13*) and model projections (*14*, *15*) that attribute population and richness declines to different types of land-use change, including reductions in forest cover. Yet, space-for-time methods may not accurately represent the effects of global change drivers, because they do not account for ecological lags (*8*, *16*, *17*) and community self-regulation (*18*). Furthermore, ongoing controversy about the diverse impacts of habitat fragmentation on biodiversity (*19*–*21*) could be in part attributable to a lack of observational data from sites encompassing the full spectrum of forest fragmentation. Recent global-scale datasets of past land cover reconstructions (*22*) and contemporary high-resolution remote-sensing observations (*23*, *24*) provide an unique opportunity to quantify landscape-scale decreases and increases in forested areas around the world (hereafter, "forest loss and gain"). By integrating forest loss estimates with over five million population and biodiversity observations (*25*, *26*, Fig. 2A), our analysis provides new insights into the influence of land-use change on local-scale population and biodiversity change around the planet.

In our study, we set out to conduct a global extent attribution analysis of the influence of forest cover change on population and biodiversity change (Fig. 1). We quantitatively tested specific predictions of the extent and pace of landscape-scale forest loss impacts on species' populations and ecological assemblages across terrestrial ecosystems around the planet (Figs. 1-2, Table S1 and Supplementary Materials and Methods (*27*). Land-use change, and particularly forest cover loss, alters habitat and resource availability (*12*, *28*, *29*) and is a global threat for the persistence of terrestrial species (*32*, Figs. 2, S12). We thus predicted the greatest impacts on populations and biodiversity when time series monitoring encompasses the 10-year period that included the largest reduction in forested areas at each site (calculated between 850 and 2015, hereafter "all-time peak forest loss"). We also expected greater population and species richness declines and higher turnover after, relative to before, contemporary peak forest loss - the year of the largest reduction in forested area within the duration of each time series. Finally, species with longer generation times typically respond more slowly to environmental change (*31*). We thus predicted lags in ecological responses to forest loss to increase with longer generation times across taxa.

We measured landscape-scale historic and contemporary forest loss by integrating information from the Land Use Harmonization (*30*) and Global Forest Change (*23*) databases We also examined whether our results were consistent across land-use change data sources using the ESA Landcover (*28*) and KK09 (*29*) databases. We compared historic and contemporary forest loss with temporal population change (trends in the numerical abundance of species) and biodiversity change (trends in species richness and turnover in assemblage composition, Figs. 1-2). We analyzed 2,729 populations of 730 species and biodiversity change in 3,361 ecological assemblages (Figs. 2A-3). We measured population change using the Living Planet Database that includes 133,092 records of the number of individuals of a species in a given area over time (*25*), and biodiversity change using the BioTIME database that comprises 4,970,128 records of the number and abundance of species in ecological assemblages over time (*26*). Together, these time series represent a range of taxa including amphibians (388), birds (5,090), mammals (266), reptiles (76), invertebrates (80) and plants (187) and 2,157 sites which cover almost the entire spectrum of forest loss and gain around the world (Fig. 2B). We used a standardized cell size of 96 km^2 to match response variables (population change, richness change and turnover) to landscape-scale forest change but note that analyses were robust to the spatial scale over which we calculated forest change (see Supplementary Materials and Methods (*27*) and Figs. S13-14).

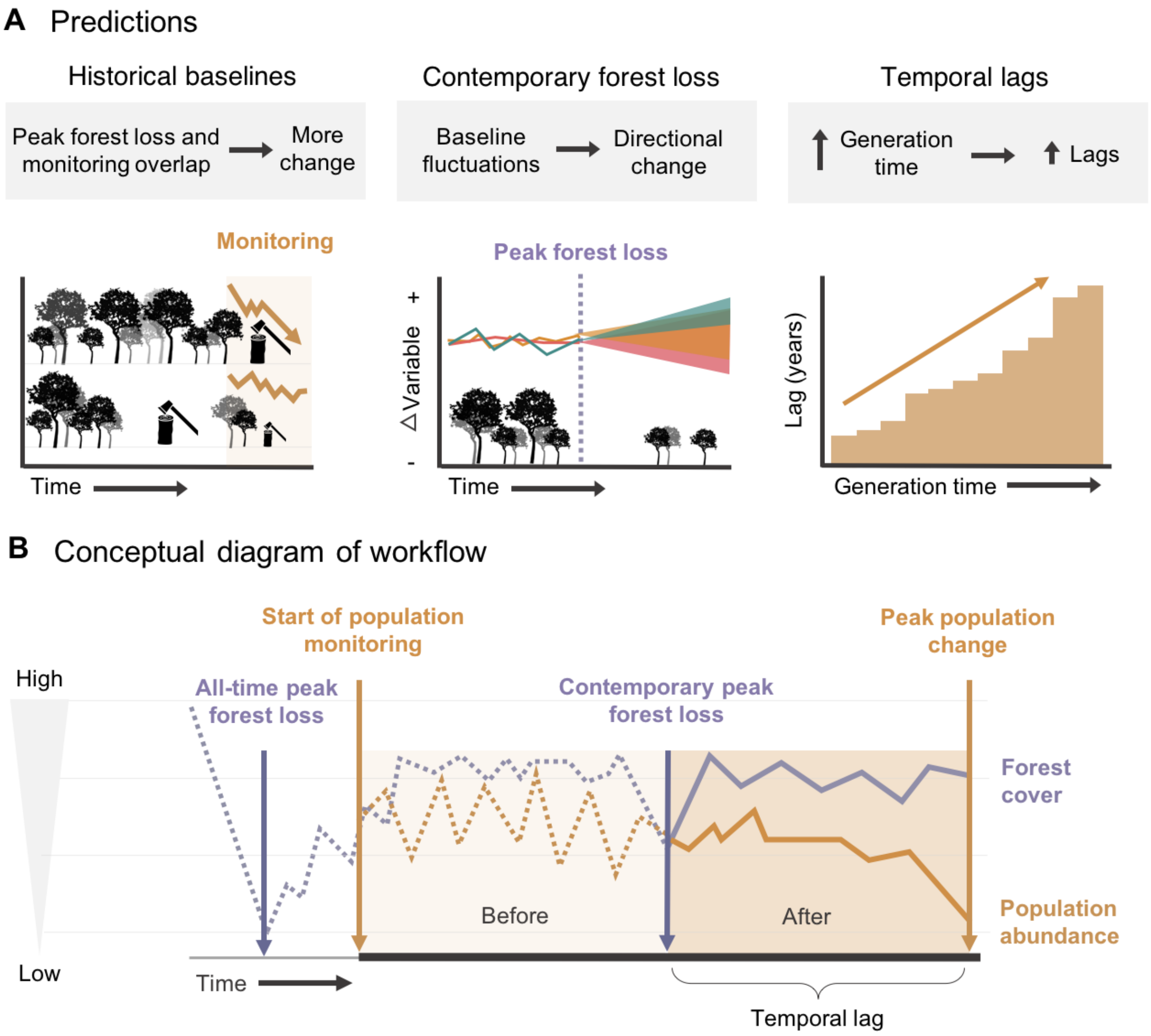

Fig 1. Influence of forest loss on population and biodiversity change. We tested three pathways through which forest loss can influence the population abundance of species and the richness and turnover of ecological assemblages: historical baselines of forest loss, timing of contemporary forest loss and temporal lags in population and biodiversity responses. **A**, Conceptual diagram of our predictions outlined with respect to population change, richness change and turnover (temporal species replacement). **B**, Analytical workflow for determining all-time and contemporary peak forest loss and temporal lags (further detail in Supplementary Materials and Methods sections one through three, (*27*).

We carried out the following workflow for our global assessment of the consequences of forest cover change for population and biodiversity trends over time. To relate population and biodiversity change to historic forest loss, we quantified the baseline all-time peak forest loss at each site. To relate population and biodiversity change to contemporary forest loss, we compared population and biodiversity change before and after contemporary peak forest loss. To investigate temporal lags, we quantified the time period between contemporary peak forest loss and maximum change in populations and assemblages detected after peak forest loss has occurred at each site (Fig. 1B). We calculated population change (μ) using state-space models that account for observation error and random fluctuations (*34*), and richness change (slopes of rate of change over time) using mixed effects models. We quantified temporal change in species composition as the turnover component of Jaccard's dissimilarity measure (change due to species replacement, *31*). Turnover is often independent of changes in species richness (*9*) and is the dominant component of compositional change across time series of ecological assemblages (*36*). We used a hierarchical

Bayesian modelling framework, with individual time series nested within biomes (*37*) to account for the spatial structure of the data (see Supplementary Materials and Methods for details, *27*).

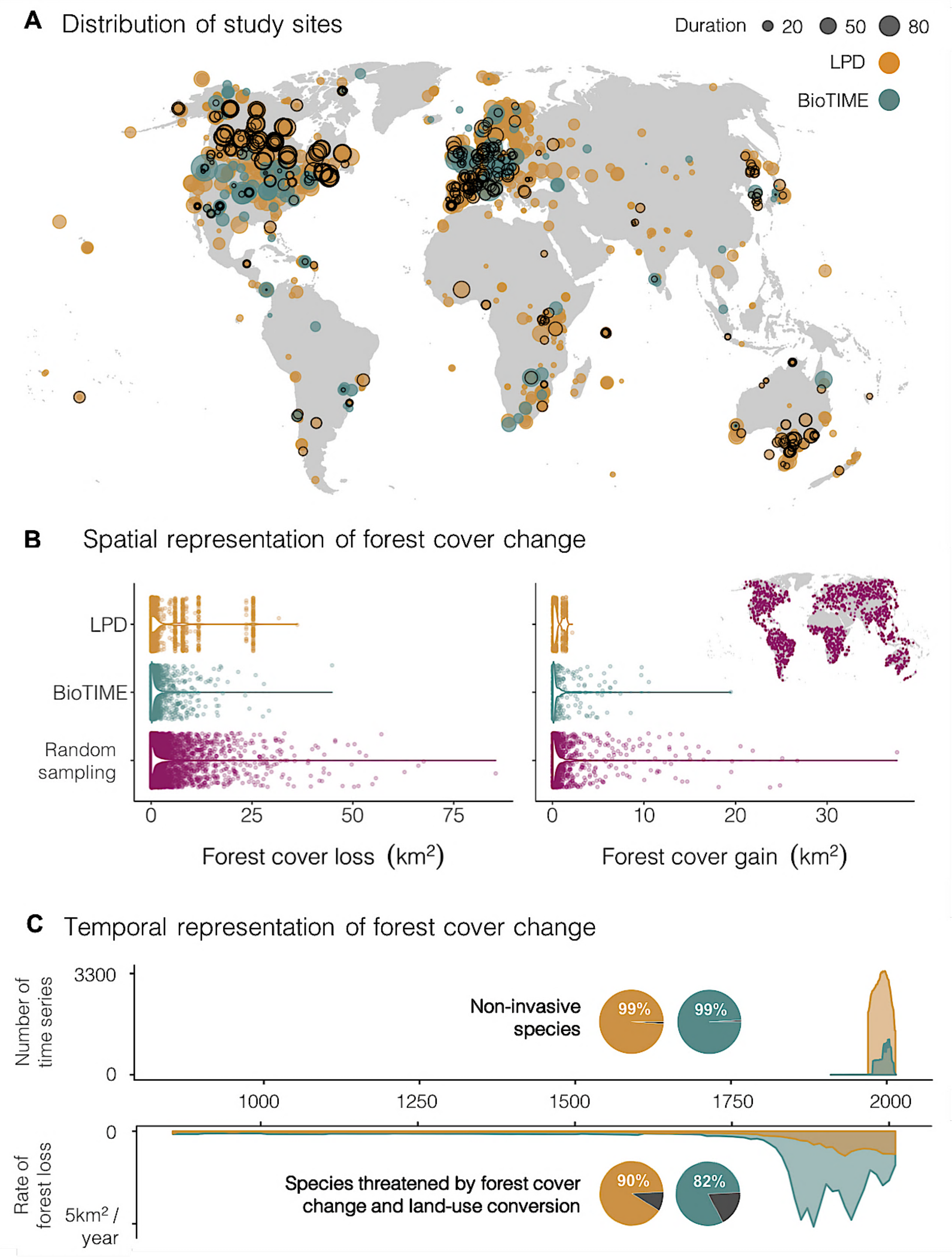
A
Distribution of study sites
Duration
20
50
80
LPD
BioTIME
B
Spatial representation of forest cover change
LPD
BioTIME
Random sampling
0
25
50
75
Forest cover loss (km^2)
0
10
20
30
Forest cover gain (km^2)
C
Temporal representation of forest cover change
Number of time series
3300
0
Non-invasive species
99%
99%
1000
1250
1500
1750
2000
Rate of forest loss
0
5km^2 / year
Species threatened by forest cover change and land-use conversion
90%
82%

Fig. 2. Population and biodiversity monitoring over time broadly spans the global variation in forest cover change. A, Locations and duration of 542 Living Planet Database (LPD) and 199 BioTIME studies, containing 6,090 time series from 2,157 sites (black outline shows sites that were forested at the start of the monitoring (1,247 sites); see Table S1 for sample size in each woody biome). **B**, 44% of all time series experienced historic or contemporary forest loss of comparable magnitude to forest cover change across a simulated random sample of geographical locations (shown on map inset in **B**) from the global distribution of forest cover loss and gain. We did not detect directional effects of the magnitude of forest gain across monitored sites (Figs. S4-S6). **C**, the number of time series increases over time (top), but the rates of forest loss were often higher before the start of monitoring (bottom, for variation in monitoring periods among time series, see Figs. S2-3). Insets in panel **C** show the proportion of study species that are not classified as invasive (top) and that are threatened by land-use change, based on species' IUCN threat assessments (bottom, see Fig. S12 for details).

Historical baselines

In line with our first prediction ("historical baselines"), we found that local-scale population declines were most pronounced when the monitoring occurred during the period of all-time peak forest loss (Figs. 1B and 3B-C). For many of the sites represented by the time series we studied, dramatic changes in forest cover occurred in the last two centuries, with all-time peak forest loss in regions like Europe and North America typically in the early 1800's, before biodiversity, population and satellite monitoring had begun (Figs. 2C and 3B). These time series captured over half of the spectrum of contemporary forest cover change around the world, in contrast to previous criticisms of these data underrepresenting areas with anthropogenic impact (*38*, Fig. 2B-C and

3B). Yet, in only approximately 5% of monitored time series forest loss led to a conversion in the dominant habitat type (*e.g.*, from primary forest to urban areas). Habitat conversions corresponded with both gains and losses in populations and biodiversity, with the highest rates of turnover when primary forests were converted to agricultural and urban areas, or to secondary forests (Fig. S17). The links between historical baselines, the timing of all-time peak forest loss and resulting ecological change emphasize the need for a long-term perspective to quantify the complexity of biodiversity change in the Anthropocene (*11*, *17*).

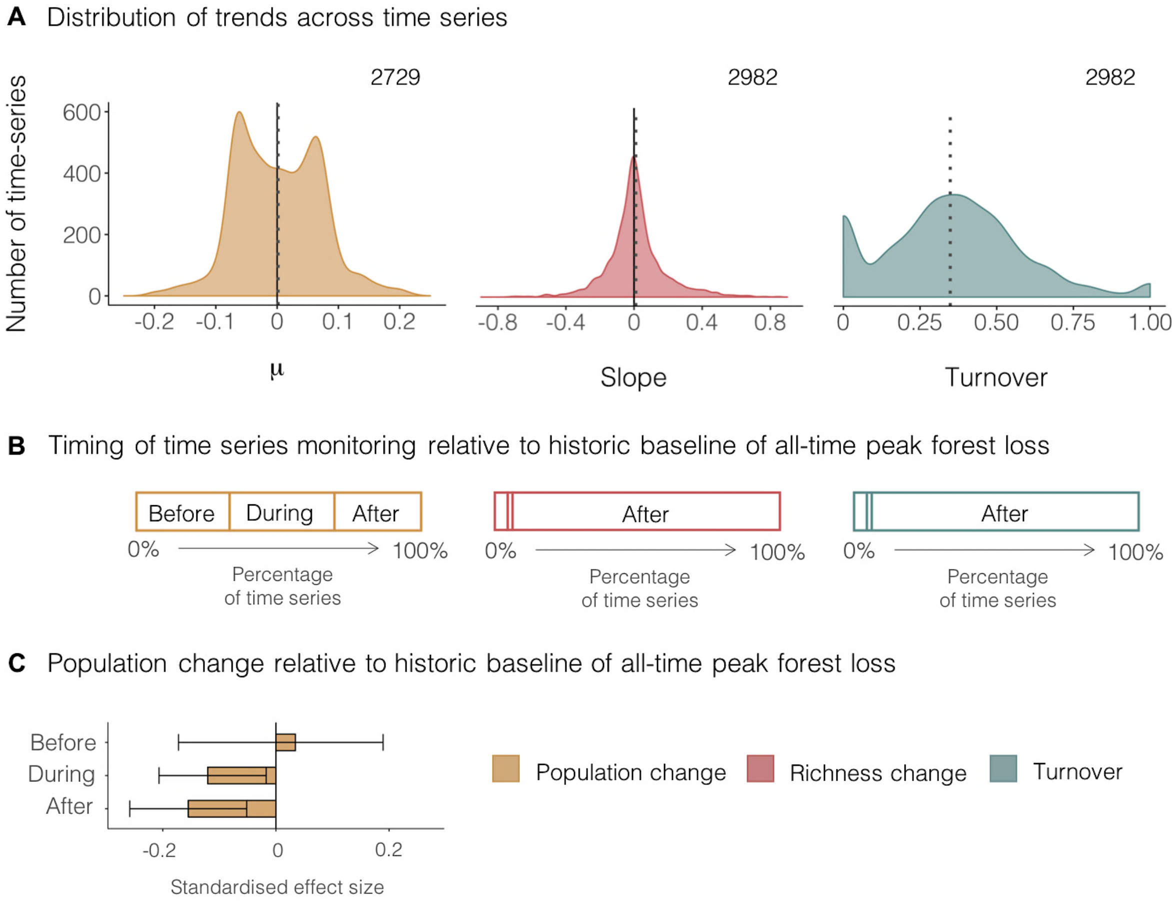

Figure 3. Heterogeneity in population and biodiversity trends and land-use histories from sites around the world. A, All three metrics of ecological change (population change, richness change and turnover) show heterogeneous distributions across sites. **B**, Population monitoring

occurred at different time periods relative to all-time peak forest loss (for 33% of sites before, for 37% during and for 30% of sites after), whereas biodiversity monitoring predominantly started after all-time peak forest loss had occurred (94% of sites). **C**, Population declines were most acute when all-time peak forest loss occurred during the population monitoring period (slope = -0.01, CI = -0.01 to -0.01; see Table S2 for model outputs). Low sample size for the 'before' (101) and 'during' (38) categories precluded a similar analysis for richness change and turnover. Numbers on **A** show sample size (i.e., number of time series).

Contemporary forest loss

Contrary to our second prediction ("contemporary forest loss"), we found that forest loss acted as a catalyst amplifying both increases and decreases in local-scale populations and assemblages over time (Figs. 3-4 and S4-6, 9-10). Across time series, more than half of all populations and assemblages (61%) experienced higher rates of change after the largest forest loss event within each time series. Contemporary peak forest loss intensified population declines, population increases and richness losses, but not richness gains, relative to the period before peak forest loss (Fig. 4). In nearly a third of time series (32%), more than 10% of the species in the assemblage at the time of contemporary peak forest loss were replaced by new species by the end of the time series (Fig. 4G-H). The assemblages that experienced the most richness change also experienced the most turnover (Pearson's correlation = 0.37, 95% confidence intervals = 0.31 to 0.43). The influence of contemporary peak forest loss on population and biodiversity change was not strongly correlated to the magnitude of the specific forest loss event (Figs. S4-6). Our findings indicate a wide spectrum of population and biodiversity responses to forest loss that might be overlooked without accounting for temporal dynamics and lagged responses (*12*, *13*, *15*, *39*).

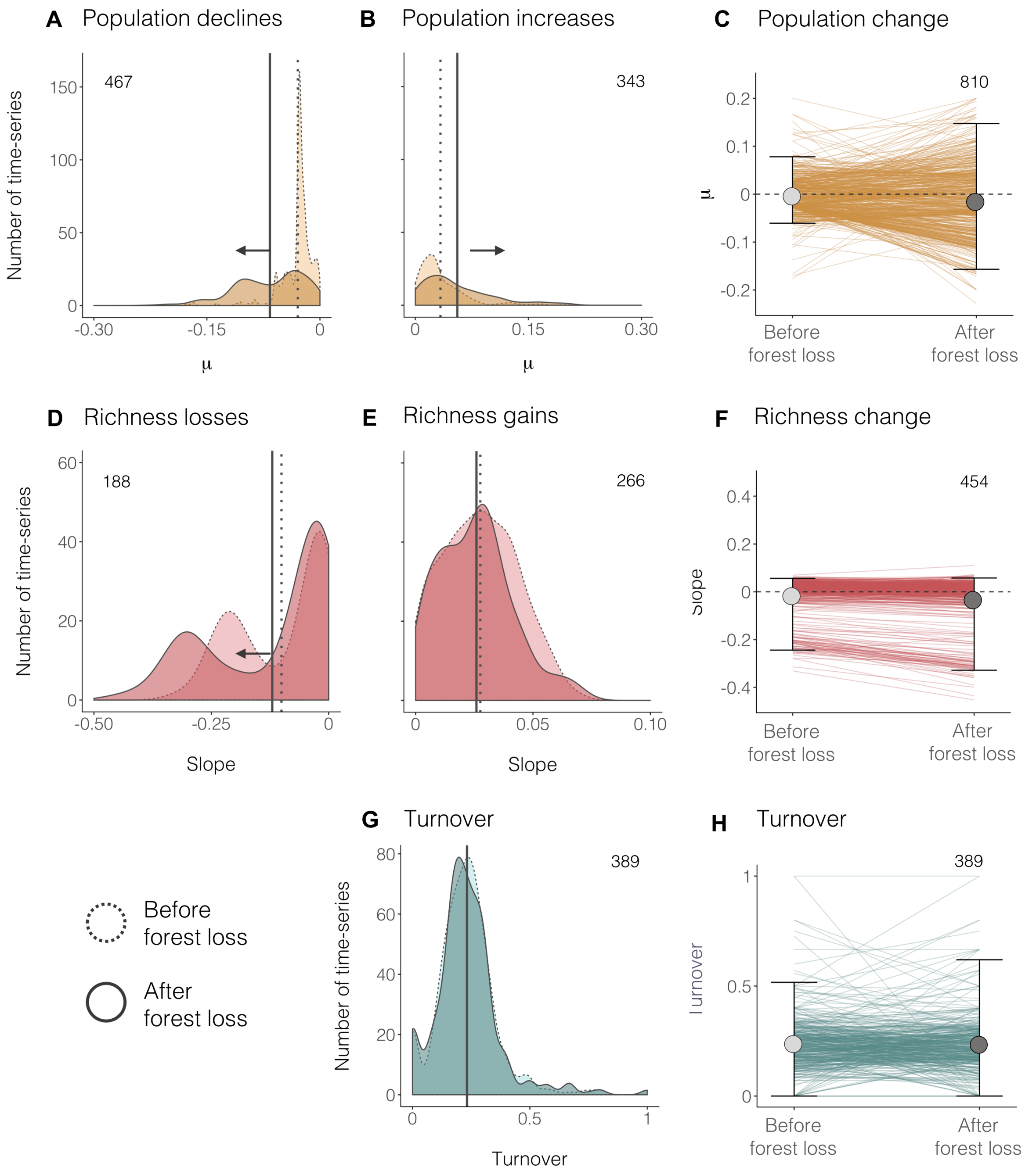

Fig. 4. At the site level, population and biodiversity change increase after contemporary peak forest loss. In total, population and richness change increased across 61% and decreased across 180 39% of the 1,653 time series for which baseline comparisons were possible (i.e., the time series were long enough to include at least five years before and after forest loss). Only turnover included

instances of no difference in the amount of change before and after peak forest loss (6% of time series). Distributions compare **A**, population declines (μ), **B**, population increases (μ), **D**, richness losses (slopes), **E**, richness gains (slopes) and **G**, turnover (Jaccard's dissimilarity) in the periods before and after contemporary peak forest loss, the largest forest loss event during the monitoring of each site. Vertical lines over distributions show the mean for each category (dotted – before; solid – after). Temporal trends before and after peak forest loss (**C**, **F**, **H)** are indicated with lines for individual time series. Light and dark grey points and error bars show mean values and 2.5 and 97.5% quantiles. Duration varied among time series but was consistent for each individual time series (*i.e.*, *n* years before forest loss = *n* years after forest loss, n ≥ 5 years; see Fig. S8 for relationship between duration and number of survey points). Numbers on plots indicate sample size. See Table S2 for model outputs.

Temporal lags

In line with our third prediction ("temporal lags"), we found evidence for up to half-century ecological lags in local-scale changes in population abundance, species richness and turnover following contemporary peak forest loss (Fig. 5). On average, we documented maximum change in populations and ecological assemblages six to 13 years after forest loss across taxa. Yet, nearly half of population and biodiversity change (40%) happened within three years of peak forest loss, demonstrating that rapid shifts in populations and assemblages occur frequently after habitat change (Figs. 5, S7). Consistent with our prediction, 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 and birds, Fig. 5B, Table S2). Population declines and increases occurred on similar timescales (Fig. 5C). Losses in species richness lagged behind gains by approximately half a year (slope = 0.5, CI = 0.1 – 1.05), indicating that extinction debts and immigration credits accumulated at roughly the same speed across taxa. The similar pace and temporal delay of population declines and increases, and richness gains and losses could help to explain previous findings of community self-regulation (*18*) and no net population change (*2*, *3*, *10*) and richness change (*5*, *6*) at local scales. Temporal lags in biodiversity change have also been observed in post-agricultural forests (*4*, *40*) and fragmented grasslands (*31*), where agricultural activity has ceased decades to centuries ago, yet richness and assemblage composition change continue to the modern-day. Overall, our results indicate that increasing rates of land-use change in the Anthropocene (*41*, *42*) will alter ecosystems on both short- and long-term timescales that need to be captured in ongoing and future biodiversity monitoring.

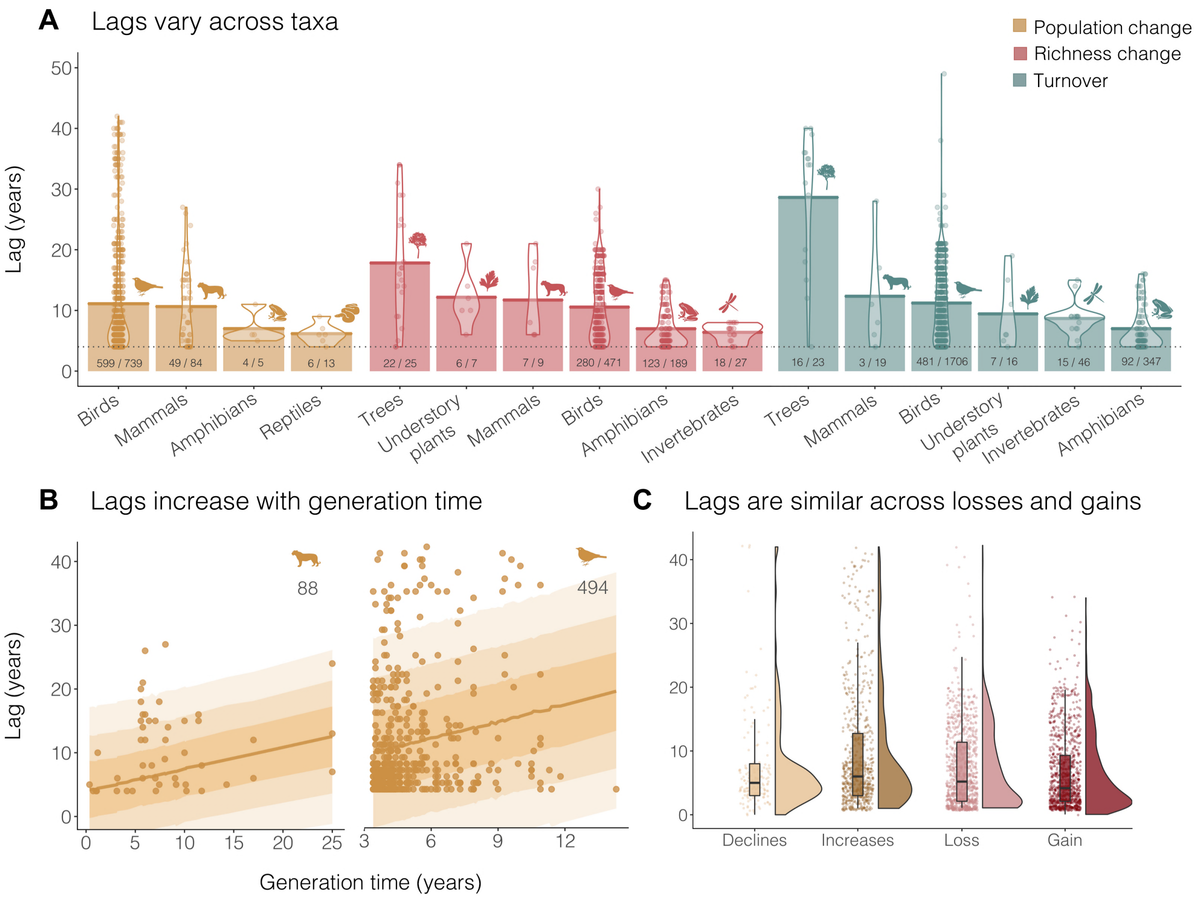

Fig. 5. Temporal lags in population and biodiversity change following contemporary peak forest loss. Population and assemblage change after contemporary peak forest loss may be delayed by up to half a century, with taxa and species with long generation times showing the longest temporal lags. **A**, We categorized lags as time periods of three (dashed horizontal line) or more years between peak forest loss during the monitoring for each time series, and peak population/biodiversity change (Fig. 2B, sample size was 841 time series for population change, 728 for richness change and 2,157 for turnover). Bars show mean lag for each taxon; violins show the distribution of lag values and the points are lag values for each time series. Numbers on bars indicate how many time series experienced lags out of the total sample size for each taxon. **B**, Temporal lags in mammal and bird population change increased with longer species' generation

times. **C**, Temporal lags were similar across population declines and increases, and species richness losses and gains. See Table S2 for model outputs.

Heterogeneity in responses to forest cover loss could be due to a number of factors, including: i) temporal lags in population or assemblage responses as observed in our study and elsewhere (*17*, *31*), ii) context specific responses to forest loss, such as the same amount of habitat change corresponding to biodiversity declines at one site, but increases at another (*13*, *43*, *44*), and iii) interactions with other drivers occurring simultaneously with forest loss (*45–47*). Our finding that forest loss was concurrent with both declines and increases in populations and assemblages is consistent with the varied and often positive effects of habitat fragmentation on biodiversity metrics such as species richness (*19*). However, forest loss occurring outside of the period of population or biodiversity monitoring, as well as the type of woody vegetation being gained and lost, might influence our ability to detect a causal link between forest loss and biodiversity change (*17*, *48*). Increases in woody vegetation caused by agroforestry or plantations might not reflect ecosystem recovery such as with natural succession after forest cover loss (*49–51*). Our finding that forest cover gain did not directly correspond with gains in population abundance and species richness highlights the need for high-resolution temporal data of the specific vegetation types constituting forest cover changes around the world. The complexity and heterogeneity of forest cover change effects on biodiversity (*13*, *43*, *52*, *53*) demonstrate that caution is warranted with recent calls for global afforestation as a climate change mitigation tool (*54*).

Variation in species' vulnerability to forest cover loss (*43*, *52*) may be contributing to the wide spectrum of population and biodiversity responses to shifts in forest cover. Species that have experienced frequent habitat disturbance during their evolutionary history might be more resilient to land-use change, whereas novel habitat alterations could have a greater influence on species' persistence and abundance (*13*, *43*, Fig. 3). In a *post-hoc* test, we found that in forest-dominated sites, where past disturbances were likely less frequent, declines in species' abundance were more frequent than increases, whereas richness change and turnover did not show directional trends (Fig. S16). Additionally, in our study, rare and common species, as defined by their range size, mean population size and habitat specificity (*55*), responded in similar ways to forest loss (Figs. S11-12). In contrast to this result, space-for-time comparisons that do not account for temporal dynamics and lagged responses have found that land-use change impacts rare species more negatively than common species (*56*). Accounting for both inter- and intraspecific heterogeneity in species' vulnerability to forest cover change is key when scaling from localized impacts of human activities to global-scale biodiversity patterns and attribution of change (*1*, *19–21*, *39*, *43*, *52*).

Taxonomic, spatial and temporal imbalances in sampling can make large-scale attribution analyses of biodiversity trends and global change drivers challenging and influence the inferences we draw from such studies (Figs. S2-3, 8, 9, 11-14). For this reason, we explored in greater detail three specific challenges of our terrestrial biodiversity attribution analyses. First, tropical species and locations are under-represented in current open-source temporal biodiversity databases (Fig. 2A, *38*). In a *post-hoc* test, we found that in the tropics, where there is intense, often unprecedented forest loss, the effects of forest loss were stronger and more negative across sites with available data, relative to the rest of the globe (Figs. S9-10, Table S1-2). Second, the spatial scales at which biodiversity is monitored (from 1 m^2 to 25 x 10^8 km^2) and the resolution of forest cover datasets (from 30 m to ~20 km, Figs. S13-14) could introduce spatial mismatches between the driver and response. Nevertheless, we found that the heterogeneous relationships between richness change, turnover and forest loss were consistent across forest loss calculated on scales from 10 km^2 to 500 km^2 (Fig. S16A-B). Third, temporal mismatches and lags (Figs. 1C and 5) can obscure relationships between forest loss and population and biodiversity change. We found that attribution signals were strongest when a peak in forest loss occurred during the time series monitoring (Figs. 3 and 4). Our results indicate that biodiversity assessments and global change attribution analyses will be improved by better spatial and temporal matching of biodiversity and environmental impact data.

In summary, our analysis reveals an intensification of both increases and decreases of populations and biodiversity by up to 48% after forest loss at sites around the planet. This finding demonstrates heterogeneity in the influence of forest cover change on populations and ecological assemblages and challenges the assumption that land-use change predominantly leads to population declines and species richness loss (*12*, *14*, *39*). A current assumption underlying existing projections of biodiversity responses to land-use change (*12*, *14*) is that space-for-time approaches accurately reflect longer-term population and biodiversity dynamics (*41*). In contrast, we found temporal lags of up to half of a century in population and biodiversity change following forest loss that differed across taxa and generation times. Our analyses highlight that the local-scale responses of populations and assemblages to forest cover loss and gain are complex and variable over time. Incorporating the full spectrum of population and biodiversity responses to land-use change will improve projections of the future impacts of global change on biodiversity and thus contribute to the conservation of the world's biota during the Anthropocene.

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Data and materials 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 (*25*, *26*). 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 (*22*), the Forest Cover Change Database (*23*) and the MODIS Landcover Database (*24*).

Supplementary Materials and Methods References are [57-272].

Supplementary Materials and Methods List:

- Materials and Methods
- Figs. S1-S17.
- Tables S1-S3.