Impacts of past abrupt land change on local biodiversity globally

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Abrupt land change, such as deforestation or agricultural intensification, is a key driver of biodiversity change. Following abrupt land change, local biodiversity often continues to be influenced through biotic lag effects. However, current understanding of how terrestrial biodiversity is impacted by past abrupt land changes is incomplete. Here we show that abrupt land change in the past continues to influence present species assemblages globally. We combine geographically and taxonomically broad data on local biodiversity with quantitative estimates of abrupt land change detected within time series of satellite imagery from 1982 to 2015. Species richness and abundance were 4.2% and 2% lower, respectively, and assemblage composition was altered at sites with an abrupt land change compared to unchanged sites, although impacts differed among taxonomic groups. Biodiversity recovered to levels comparable to unchanged sites after >10 years. Ignoring delayed impacts of abrupt land changes likely results in incomplete assessments of biodiversity change.
Natural and anthropogenic processes change the terrestrial surface of the Earth, which have been shown to impact biodiversity and ecosystem services. Previous studies have found that differences in land-surface conditions reduce local biodiversity globally. However, biodiversity studies often ignore the impacts of past land change. Such change encompasses natural (e.g., fires, storms) and/or human-driven (e.g., agricultural expansion, urbanisation) changes in land use and land cover. Simulations and experiments have demonstrated that land changes of greater magnitude have larger impacts on the number of species and individuals present within local assemblages, and potentially reduce resilience. The impacts of land change on species assemblages depend on species' ability to disperse and recover.\(^\text{[22]}\) Past land changes have been shown to cause 'legacies' affecting ecosystems and species to the present day. Most previous global studies investigating abrupt land changes in the past have used descriptive study-specific categories of "land changes", e.g., wild fire, flooding or cultivation, thus hindering comparisons among studies, and preventing predictions. To assess the impacts of abrupt land change on local biodiversity more generally, comparable quantitative measures of "land change" are needed.

The availability of time series of satellite imagery enables the detection and quantification of land changes globally. Land change can be quantified as abrupt shifts in intra- and inter-annual dynamics of remotely-sensed photosynthetic activity measured by vegetation indices. Abrupt shifts in magnitude and trend and varying time passed for species richness exhibit expectation we found that sites with an abrupt land change up to 5 years before biodiversity sampling had on average 6.6% fewer species compared to unchanged sites (Fig. 2a, c). After more than 10 years had passed, biodiversity measures were comparable to unchanged sites (Fig. 2b, d, f), except for local species richness at sites with positive shifts in magnitude (4%; Fig. 2b). Overall, we found similar impacts of shifts in magnitude and trend and varying time passed for species richness between mixed effect models for magnitude and trend (Pearson's \(r\) between impacts = 0.71), abundance (\(\Delta\)AIC = 2.64, \(r = 0.61\)), and evenness (\(\Delta\)AIC = 5.66, \(r = 0.98\)).

Abrupt land changes affect composition of assemblages. Species assemblages at sites with larger abrupt shifts in magnitude were less similar in composition to unchanged sites. Especially sites with a shift in magnitude of >50% EVI loss or gain were on average less similar (\(z = 0.04\)) compared to unchanged sites. Overall, we found similar impacts of shifts in composition (\(\Delta\)AIC between mixed effect models for magnitude and trend = 2.85, Pearson’s \(r\) between impacts = 0.66), abundance (\(\Delta\)AIC = 2.46, \(r = 0.42\)), and evenness (\(\Delta\)AIC = 3.03, \(r = 0.65\)).

Impacts of abrupt land changes vary among taxonomic groups. Sites with a positive shift in magnitude had significantly fewer species of plant (\(z = -4.75, \text{df} = 613, p < 0.0001\)), bird (\(z = -2.36, \text{df} = 605, p = 0.018\)) and reptile (\(z = -0.14, \text{df} = 95, p = 0.04\)) compared to unchanged sites (Fig. 4a). Particularly sites with a negative shift in trend had significantly fewer species of plant (\(z = -5.82, \text{df} = 918, p < 0.0001\)).

Results

Local biodiversity at sites with past abrupt land changes. Sites at which an abrupt land change was observed contained on average 4.2% fewer species (Standard Error (SE): 1.3%, \(\chi^2 = 10.3, \text{df} = 3, p < 0.01\)), 2% fewer individuals (SE: 1.3%, \(\chi^2 = 72.9, \text{df} = 3, p < 0.001\)), and species assemblages were 1% less even (SE: 0.6%, \(\chi^2 = 42.8, \text{df} = 3, p < 0.001\)) compared to unchanged sites (Fig. 2). Sites with larger abrupt shifts in magnitude and trend had fewer species and individuals than unchanged sites regardless of direction of abrupt land change (Fig. 2a, c). Sites with >50% loss or gain in EVI had on average 15.5% (SE: 5.4%) or 10.5% (SE: 3.4%) fewer species, and 10.7% (SE: 3.8%) or 5% (SE: 3%) fewer individuals than unchanged sites (Fig. 2a, c). Compared to unchanged sites, species assemblages were less even at sites with larger abrupt losses in EVI, but not at sites with larger gains in EVI (Fig. 2e).

Local biodiversity can recover after abrupt land changes. We hypothesize that with more time passed local biodiversity recovers to levels comparable to unchanged sites. In line with our expectation we found that sites with an abrupt land change up to 5 years before biodiversity sampling had on average 6.6% fewer species compared to unchanged sites (Fig. 2b, d, f). After more than 10 years had passed, biodiversity measures were comparable to unchanged sites (Fig. 2b, d, f), except for local species richness at sites with positive shifts in magnitude (4%; Fig. 2b). Overall, we found similar impacts of shifts in magnitude and trend and varying time passed for species richness between mixed effect models for magnitude and trend (Pearson’s \(r\) between impacts = 0.71), abundance (\(\Delta\)AIC = 2.64, \(r = 0.61\)), and evenness (\(\Delta\)AIC = 5.66, \(r = 0.98\)).

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Fig. 1 Examples of abrupt land change and distribution of sites. a Remotely-sensed time series of monthly enhanced vegetation index (EVI; green points) of the same duration at an unchanged site (top panel) and at four sites with an abrupt shift in magnitude (i.e., gain or loss in EVI). Linear (black lines) and seasonal (dark green lines) fits of the change detection algorithm are shown. b Location of 5563 sites from 377 studies in the PREDICTS database with an abrupt land change in the monitoring period (since 1982) of the Landsat 4–8 missions with a relative shift in magnitude (location of sites with shifts in trend see Supplementary Fig. 1). For ease of viewing, the location of 10,102 sites without an abrupt land change have been omitted. Map shown in Eckert IV equal-area projection.

Discussion

We found species assemblages to be negatively impacted by past abrupt land change. Larger changes on land caused greater reductions in local biodiversity (Fig. 2a–c) regardless of whether shifts in magnitude or trend of photosynthetic activity (EVI) were positive or negative, suggesting general impacts of past abrupt land change on biodiversity11,13 likely caused by biotic lag effects4,17,19. Abrupt land changes with large (>50%) losses or gains in EVI have caused immediate and time-delayed local extinctions16,38,39 and reduced the abundance and dominance of persisting species (Fig. 2b, c), which may ultimately affect ecosystem functioning9,13. Local biodiversity at sites with an abrupt land change recovered to levels comparable to unchanged sites after >10 years23,24, although local species richness did not recover at sites where EVI had increased (Fig. 2d). Abrupt land changes can alter the composition of species assemblages with early colonizing and non-native species often outperforming or replacing many persisting species40–42, which could explain the observed impacts on species assemblage evenness (Fig. 2c) and compositional similarity (Fig. 3). However, to more fully disentangle the impacts of abrupt land change on local biodiversity, before-after, control-impact (BACI) estimates of biodiversity are needed43, which are currently unavailable globally. Overall, our results suggest that abrupt land changes in the past continue to influence present species assemblages globally.

What drives abrupt land change events? Abrupt land change, identified by shifts in magnitude and/or trend of photosynthetic activity, can be caused by anthropogenic deforestation31, land intensification41,45, or degradation46,47, or by natural factors such as climatic anomalies48, nutrient deposition, or CO2 fertilization49. Most PREDICTS sites were modified by humans37,50 and it is therefore likely that most detected land changes were caused by humans. Future studies should attempt to distinguish and disentangle the impacts of natural and anthropogenic abrupt land changes31 and investigate whether different drivers of land change, such as agricultural conversion or natural fires, have differential impacts on local biodiversity. Furthermore, the duration of land change, e.g. brief leaf die-off vs permanent removal of vegetation, and how this differentially impacts species may be worthwhile investigating8.

Detecting and quantifying abrupt land changes is challenging. Here, we focussed on detecting abrupt land change as shifts in magnitude or trend36, but not all land change is abrupt52 or—such as understory thinning and selective logging—can be detected in time series of remotely-sensed photosynthetic activity33,54. Similar to previous studies we assessed only the impact of the single largest shift in magnitude or trend2,23, while different sequences of land change may also affect local biodiversity8. Future studies quantifying abrupt land change globally could benefit from better access to, or fusion of, available satellite data to attain higher temporal and spectral resolution55,56.

In conclusion, we demonstrate that compared to unchanged sites local biodiversity is considerably reduced because of abrupt land changes in the past, potentially affecting the stability and functioning of ecosystems13. Ignoring delayed biodiversity responses to abrupt land changes means that contemporary biodiversity changes, loss and recovery, are underestimated14,57. Conservation practitioners need to consider the impacts of biotic lag effects to ensure global and regional assessments (e.g. those by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES]) fully capture biodiversity change57. Remote sensing can assist in quantifying attributes of abrupt land change over large spatial and temporal scales. Our analytical framework can be expanded to assess spatial prioritization of habitat restoration plans or to support scenario-based modelling23 to predict the impacts of abrupt land change on local biodiversity.
Local biodiversity impacts varied with attributes of abrupt land change. Differences in a, b local species richness, c, d total abundance, and e, f the probability of interspecific encounter (PIE) at sites with an abrupt land change (squares, diamonds) relative to unchanged sites (black circles). a, c, e Estimates are given separately for shifts in magnitude (squares) and in EVI trend (diamonds). b, d, f Impacts on biodiversity measures of time passed between an abrupt land change and sampling of biodiversity for EVI shift in magnitude (squares) or for trend differences (diamonds). Separate models were fitted for shifts in magnitude and in trend relative to unchanged sites (points). Error bars show fitted standard errors and asterisks statistical significance (\( p < 0.05, ** p < 0.01, *** p < 0.001 \)) from the hierarchical mixed effects models. For number of sites and studies for each bin and biodiversity measure see Supplementary Figs. 2, 3 and Table 1. Source data are provided as a Source Data file.

Methods

**Biodiversity data.** We used published data from the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) database\(^6^7\), which includes species’ presence and abundance data from ‘studies’ with at least two spatially-explicit ‘sites’, information on the date of sampling, and local land-use and/or land-use intensity\(^7\). We simplified the original PREDICTS land use and land-use intensity information\(^7,27\) by allocating each site to one of three broad land-use categories: primary vegetation (PV, i.e. primary [non-] forest), secondary vegetation (SV, i.e. mature, intermediate, young and indeterminate age secondary vegetation) or human-dominated vegetation (HDV, i.e., plantation forest, crop-land, pasture, urban). Studies were grouped into eight broad taxonomic groups based on the sampled taxa: plants, fungi, ground-dwelling invertebrates (e.g., soil-fauna, snails, beetles), flying invertebrates (e.g., butterflies, bees, dragonflies), amphibians, reptiles, birds or mammals.

We assessed four measures of local biodiversity that complement each other and have previously been shown to be sensitive to abrupt land change\(^22,27\). For each site in the PREDICTS database, we calculated within-sample species richness and, where data on abundance were available, log\(_{10}\) total abundance of individuals, adjusted by sampling effort following Newbold et al.\(^29\). After visual inspection, we removed one outlier study (a study of understory plants, ID “DL1_2012_CalvinoCancela”) from further analyses because of its unique way of measuring abundance (using biovolume). As a measure of assemblage evenness, we calculated the arcsine square root transformed probability of an interspecific encounter (PIE), which quantifies the probability of two individuals randomly chosen from an assemblage representing different species\(^60\). As a measure of turnover in species assemblage composition within studies, we calculated the Sørensen similarity index among spatial pairs of sites within each study and land-use category\(^61\). All biodiversity measures were calculated using R code available on GitHub (https://github.com/Martin-Jung/PastDisturbance).

Species assemblages were sampled at various spatial extents defined by each study’s sampling method and land use. Following the PREDICTS data curation protocol, we assumed the allocated land use to be dominant within the reported sampling extent (maximum linear extent [MLE], in meters) of each site\(^7,27,28\). For studies without reported MLE (4779 sites, 18.3% of all sites), we used either the mean MLE for each taxonomic group and corresponding sampling method, e.g., mist netting, pitfall trapping, or the mean MLE within the same taxonomic group. To test whether these interpolated MLEs are consistent among taxonomic groups and sampling methods, we randomly removed 25% of the reported MLEs and found that the interpolated MLEs to be reasonably correlated (Pearson’s \( r = 0.73, p < 0.001 \)). We included all studies with a MLE \( \leq 3000 \) m (98.3% of all sites), approximately 100 times the nominal resolution (~30 m) of the remotely-sensed data used in this study, and removed four studies with sites located in water (rivers, coastal areas or ponds), identified by intersecting all sites with a global permanent water surface mask\(^62\), as a precaution as sites within these studies likely have low positional accuracy. We cannot rule out that some PREDICTS sites have imprecise coordinates, although we have no evidence or reason to suspect any systematic bias, taxonomically or geographically, in the coordinate accuracy or precision that could substantially affect our findings. For 96.7% of all sites in the PREDICTS database, coordinates were obtained from publications or supplied by the authors of the original studies while for the remaining studies, coordinates were worked out using the information provided in publications, followed by a detailed assessment of coordinate accuracy for all sites as part of the PREDICTS database curation\(^8\). To spatially link species assemblage with remote sensing data, we calculated a square buffer with the study-specific MLE as side lengths (MLE\(_{\text{median}} = 70 \) m; \( Q_3 = 30 \) m,
Q₄ = 200 m) around each site's coordinates as the smallest area that fully captures all grid cells of varying sampling units (e.g., point counts, line transects). Square buffers around site coordinates likely capture the area sampled best as the sampling layout of the majority of studies was rectangular.

**Remote sensing data.** We used land-surface reflectance products derived from the sensors of the Landsat 4 (1982–1993), 5 (1984–2012), 7 (1999–ongoing), and 8 (2013–ongoing) missions available within Google Earth Engine (GEE)63, based on raw United States Geological Service Landsat Collection images (Tier 1) to calculate the Enhanced Vegetation Index (EVI, as two-band version64) as a proxy of photosynthetic activity. We masked all cloud-covered grid cells (~30 m nominal resolution) using the cloud-detection output in the cfMask package65 and removed occasional snow- and water-covered grid cells, i.e. those with negative EVI values. All data preparation and extraction were performed within GEE63.

For each Landsat image and PREDICTS site we calculated the mean EVI within the rectangular buffer (j) and extracted time series of all EVI values. We removed outliers introduced by satellite sensor errors, missed cloud shadows or bad quality estimates by calculating the absolute difference of all y values from the median absolute deviation (MAD) per EVI time series66. EVI values more than a conservative threshold of two units of deviation away from the MAD or in the top 1% of all MAD estimates were set to NA66. Time series of EVI data were temporally aggregated to monthly maximum value composites to ensure equal intervals between data points and to reduce the amount of noise and missing data. Because of the ongoing consolidation of the global Landsat archive65, there can be periods of consecutively missing data, particularly before the launch of Landsat 7 in 1999 (Supplementary Fig. 5a). We truncated time series with gaps of ≥5 years of consecutively missing data, which might affect the precision of land change attribute calculations, by truncating these time series to include only the years from 1999 onwards in subsequent analyses (see Supplementary Fig. 5b). In total 25,656 sites had suitable EVI time series, with an average 18.83 (±6.7 SD) years duration containing on average 1.82 years (±1.57 SD) of consecutively missing data.

**Abrupt land change detection.** To identify the presence of abrupt land change and its attributes in EVI time series, we used the breaks For Additive Season and Trend (BFAST) algorithm34 modified to work with missing data and optimized to find the single most influential abrupt land change in a time series35. BFAST accurately detects abrupt land changes31,36 by using a multiple regression model to estimate both trend and seasonal components of a time series:

\[
\gamma(t) = \alpha + \beta t + \sum_{j=1}^{k} y_j \sin\left(\frac{2\pi t + \delta_j}{p}\right) + \epsilon, \quad \text{where } y_j \text{ is the mean EVI at time } t, \quad \alpha \text{ the intercept, } \beta \text{ the slope (i.e., trend), } p \text{ and } k \text{ the order of the seasonal term (k=2), } y \text{ the amplitude, } \theta \text{ the phase and } \epsilon \text{ the residual error.}
\]

The expected frequency to detect an abrupt land change in a time series is determined by the model to fail to converge (17% of all fitted models), we removed the seasonal component caused the model to fail to converge (17% of all fitted models), we removed the seasonal component by time series decomposition (xtpile package67) prior to fitting BFAST with a trend component only. BFAST detects abrupt land change when model residuals depart significantly (p < 0.05) from a statistical boundary67. To test for significant departure we used two complementary approaches67,68 using first, a moving sum of residuals (MOSUM) test within the monitoring period (determined by h) and second, an information-theoretic approach, the Bayesian Information criterion (BIC). All BFAST models were fitted using the bfast package (ver. 1.5.7) in R (ver. 3.5.0).67,70

For the single most influential abrupt land change detected in each time series, we calculated the relative shift in magnitude as the immediate change in EVI (minus signs/red and plus signs/blue) and time passed between abrupt land change and biodiversity sampling (axis labels as in Fig. 2); Colours, from purple to brown (in Q4 Fig. 3).

**Fig. 3 Reduced compositional similarity between sites with and without abrupt land change.** Mean similarity in species assemblage composition (Sørensen similarity index) calculated between pairs of sites within and without land change category (UC) and with an abrupt land change of (a, c) varying shifts in magnitude, or (b, d) loss or gain in EVI (minus signs/red and plus signs/blue) and time passed between abrupt land change and biodiversity sampling (axis labels as in Fig. 2); Colours, from purple to brown (in a, b), indicate more or less similar assemblage composition with unchanged sites on average relative to comparisons among unchanged sites. Numbers (in a, b) indicate the total number of studies for which pairwise comparisons between sites could be made. All estimates are transformed relative to the compositional similarity between pairs of sites without a land change (UC – UC). (c, d) Dendrograms show hierarchical clustering of all pairwise similarities based on the average Manhattan distance between pairs of sites; sites with more similar assemblage composition are in branches of closer proximity.
after an abrupt land change has been identified and \( \beta_{1j} \), the predicted estimate one month before), the difference in linear trend as increase/decrease in EVI before and after the abrupt land change (\( \beta_{2j} - \beta_{2j} \)), where \( \beta_{2j} \) and \( \beta_{2j} \) are the predicted linear trends in EVI from the BEAST model, before and after the abrupt land change, and the time passed (in months, \( t_j - t \)) between the date of the abrupt land change (\( t_j \)) and the start of biodiversity sampling (\( t_i \)). Attributes of abrupt land change were grouped into bins as follows (Supplementary Fig. 2 and Table 1): for shifts in magnitude (>50%, >25% and ≤50%, and ≤25% EVI loss or gain, Supplementary Fig. 2a), for shifts in trend (0.01, 0.05, and >0.05 lower or higher EVI trend change, Supplementary Fig. 2b) and time passed (<5, 5-10, and >10 years ago, Supplementary Fig. 2c). The three attributes of abrupt land change were only marginally correlated among each other (mean Pearson’s \( r \) ≤0.07, Supplementary Fig. 6). Sites without an abrupt land change detected by BEAST are referred to as “unchanged” sites (UC) and all studies containing only unchanged sites (10,196 sites of 262 studies) were excluded from further analyses.

Statistical analyses. We built hierarchical models comparing biodiversity measures between paired sites, i.e. those with and without an abrupt land change in the past, from the same study and sampled at the same point in time using the same sampling method to account for differences among studies71. Hierarchical generalized linear mixed effects (LME) models were fitted separately for species richness (using a Poisson error distribution), total abundance, and the PIE (using a Gaussian error distribution). For models of species richness we included an observation-level random effect (i.e., site ID) to account for overdispersion72. For each LME model we compared several candidate random-effect structures by fitting null models with combinations of different random intercepts and random slopes to determine the structure with the lowest overall Aikake Information Criterion (AIC). Random effects always included the study ID to account for study-level differences in sampling methods, optionally a spatial block ID in which sites were located, the site’s land-use category (PV, SV, HDV), the presence of an abrupt land change (yes/no) as random slope within the study, as well as the studies climatic zone (tropical, arid, temperate or continental climate) according to the Köppen Geiger classification73. Whenever a climatic zone could not be determined (for instance on small islands), we attributed studies to a zone based on latitude and a site’s terrestrial biome (1369 sites). The most parsimonious random-effect structure by AIC was identical among response variables and included — besides the study ID — the spatial block and land-use category as random intercept as well as the presence of an abrupt land change as random slope. We included the binned attributes of abrupt land change, e.g. shifts in magnitude, trend, and time passed, as fixed effects in our models with the unchanged sites (UC) as paired reference comparison. Separate models were fitted for each taxonomic group using the direction (positive or negative) of magnitude and trend shifts because of limited data availability. Full LME models were tested for significant differences (\( p < 0.05 \)) from a null model using likelihood ratio tests, while significant differences between bins were approximated by Wald statistics74. To compare estimated impacts of a shift in magnitude against shift in trend, we assessed the difference in Aikake’s Information criterion (AIC), a difference of \( \Delta \text{AIC} < 7 \) commonly indicating less support of either model being more parsimonious, and furthermore calculated ordinary Pearson correlation coefficients between their estimated models were otherwise not comparable, for instance by conventional maximum likelihood ratio tests, because of equal fixed structures. All statistical tests used were two-sided. All models were fitted using the ‘lme4’ package (ver. 1.1-14 in R ver. 3.5)74.

To estimate differences in species assemblage composition we calculated the mean compositional similarity (as quantified by the Sorenson similarity index) between all spatial pairs of sites without and with an abrupt land change in the same study and land-use category. To visualize the mean similarity for each land change attribute bin, we performed hierarchical complete-linkage clustering (‘hclust’ function in R) on Manhattan distances between estimates of compositional similarity transformed relative to the mean difference between pairs of unchanged sites.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Code availability
Codes are available at https://github.com/Martin-Jung/PastDisturbance.

Data availability
The PREDICTS biodiversity data are publicly available in the Natural History Museum Data Portal (https://doi.org/10.5519/0066354)77. All remote sensing data are accessible via Google Earth Engine (https://developers.google.com/earth-engine)78 and pre-processed time series are deposited on GitHub (https://github.com/Martin-Jung/PastDisturbance). The source data underlying Figs. 2 and 4 and Supplementary Fig 3 are provided as a Source Data file.

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Author contributions
All authors designed the study. M.J. collected and analysed the data and wrote the first draft of the paper. M.J., P.R. and J.P.W.S. discussed the results and wrote the paper.

Competing interests
The authors declare no competing interests.

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