Habitat change and biased sampling influence estimation of diversity trends

Wenyuan Zhang[1, 4, *], Ben C. Sheldon[1], Richard Grenyer[2], and Kevin J. Gaston[3]

[1]Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK
[2]School of Geography and the Environment, University of Oxford, Oxford, OX1 3QY, UK
[3]Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9FE, UK
[4]Lead contact
*Correspondence: wenyuan.zhang@zoo.ox.ac.uk

Twitter: plmyann

SUMMARY

Recent studies have drawn contrasting conclusions about the extent to which local-scale measures of biodiversity are declining, and whether such patterns conflict with the global-scale declines that have attracted much attention [1]. A key source of high quality data for such analyses comes from longitudinal biodiversity studies which sample a given taxon repeatedly over time at a specific location [2]. There has been relatively little consideration of how habitat change might lead to biases in the sampling and continuity of biodiversity time-series data, and the consequent potential for bias in the biodiversity trends that result. Here, based on analysis of standardised routes from the North American Breeding Bird Survey (3014 routes sampled over 18 years) [3], we demonstrate that major local habitat change is associated with an increase in the rate of survey cessations. We further show that routes that were continued despite major habitat changes show reduced diversity. By simulating potential rates of loss, we show that the underlying real trends in taxonomic, functional and phylogenetic diversity can even reverse in sign if more than a quarter of diversity is lost from routes that ceased, and are thus no longer included in surveys. Our analyses imply that biodiversity loss can be underestimated by biases introduced if continued sampling in longitudinal studies is influenced by local change. We argue that researchers and conservation practitioners should be aware of the potential for bias in such data and seek to use more robust methods to evaluate biodiversity trends and make conservation decisions.

KEY WORDS

Biodiversity trends, habitat change, longitudinal studies, survey cessation, sampling bias, non-random sampling, functional diversity, phylogenetic diversity.

RESULTS AND DISCUSSION

Longitudinal studies play a crucial role in understanding how biodiversity is changing in response to direct and time-lagged processes. Most studies evaluating temporal diversity trends are based on consecutive time-series records, or at least records including the beginning and the end of the objective study periods. Often, the data gaps in time-series datasets or subsets with relatively large data gaps are ignored or imputed with simple methods [4-6]. If such gaps in time series are from sites disproportionately affected by biodiversity and richness declines, they may bias the long-term data sets towards relatively undisturbed communities and underestimation of biodiversity responses to human pressure. One mechanism by which this might occur in long-term biological monitoring programmes is if the habitats in or surrounding the survey sites experience abrupt modification [7]. If the sampling of such sites ceases disproportionately as a result, locations showing the greatest biodiversity loss would tend not to be incorporated in a final dataset.

To determine the potential for impacts of major habitat change on estimating biodiversity trends, here we evaluated the association between major habitat change and cessation of sample routes of a long-term biological monitoring programme, the North American Breeding Bird Survey [BBS] [3]. BBS data are collected once per year by more than 2500 trained recorders in June over 5000 survey routes that are located randomly within physiographic strata across the continent to sample habitats that are representative of the entire continent. They have frequently been used for estimating regional-level bird population trends and prioritising species and areas for conservation action [2, 8-10]. We estimated yearly habitat change using a land cover product from the Terra and Aqua combined Moderate Resolution Imaging Spectroradiometer (MODIS), Land Cover Climate Modelling Grid (CMG) Version 6 (MCD12C1) [11] from 2001-2018 at 0.05° resolution. We then calculated the habitat change for each route as the difference between the focal year and the preceding year in the proportion of 16 habitat types around the 3014 neighbourhoods of the routes. We used multiple non-overlapping ranges to characterise the major habitat change (i.e., whether the total change of 16 habitat types is ≥5% and < 10%, ≥10% and < 15%, ≥15% and <20%, ≥20% and < 25%, ≥25% and <30%, and ≥30% of the total buffer area). For example, we would define a change from 13% wetland to 6% farmland and 7% grassland of the total neighbourhood around a route as a 10% - 15% change. In cases where habitat did change, we defined two cases: *survey ceased (habitat change) routes* were those where a survey stopped and did not restart by the end of the study period (i.e., 2018); otherwise they were defined as *survey continued (habitat change) routes* (see Figure 1 for illustration). Where necessary we calculated null randomisation distributions by reallocating the observed habitat changes randomly across all routes.

To understand how habitat loss affects diversity, we used three diversity indices calculated from the BBS data: taxonomic diversity (species richness), functional diversity as the proportion of a hyperspace defined on Elton Traits, and phylogenetic diversity via the shared root of the bird phylogeny (for full details see methods). We calculated diversity trends in all three metrics across time in two ways: the annual change between 2001-2018 by fitting regression models to time, and a comparison of 3-year periods at the beginning and end of the dataset (i.e. 2001-03 and 2016-18, to avoid the potential effect of unusual or abnormal years) as the difference of diversity between the 2016-18 and 2001-03 periods divided by diversity of the 2001-03 period. For both approaches, we estimated effects of habitat change on biodiversity by comparing the diversity trend in survey continued (habitat change) routes and survey continued (no habitat change) routes. To assess the potential effect of no longer including those sites at which surveys ceased (and for which overall biodiversity change is, by definition, unknown), we simulated a range of values (from 0-100%) of diversity loss for the single year when a survey cessation happened, with diversity change at the average rate of survey continued routes afterwards; while 100% diversity loss is an unlikely extreme scenario for this dataset, it might occur for habitat specialist taxa, and we included the full range to enable generality in our conclusions. We also simulated how overall diversity trends could be influenced across different proportions of survey ceased (habitat change) routes. In so doing we asked how the continued incorporation of these sites would have influenced the rate of change in biodiversity in the overall sample.

Habitat change-associated route cessation was a frequent, but not predominant, phenomenon in the BBS dataset: most routes that ceased did not have associated habitat change, and most habitat change was not associated with route cessation. However, we found that the minority of routes that did experience habitat change-associated cessation would be sufficient to induce significant quantitative and qualitative changes in the interpretation of overall biodiversity trends.

We found that cases of a ≥5% major habitat change associated with a survey cessation occurred in 253 out of the total 3014 BBS routes. Within the subset of 253 survey ceased (habitat change) routes, in 182 routes (72%) the survey cessation occurred one year before, or was contemporaneous with, the major habitat change (Figure 1-A), whilst in the remaining 71 routes the survey cessation occurred one year after the major habitat change (Figure 1-B). Survey cessation that was not associated with our measure of habitat change was found in 920 BBS routes. We also found ≥5% major habitat change occurred in 1535 BBS routes (52%) but was unrelated to any survey cessations; no major habitat change was detected in 1226 BBS routes (41%).

Despite being low in absolute terms, we found the cessation of survey routes to be significantly associated with local habitat change. In many cases, the frequency of survey cessation (habitat change) is approximately double what would be expected if major episodes of local habitat loss are randomised across time and space (Figure 2). Despite being significantly associated with cessation, the relationship between the amount of habitat change and route cessation is complex. As the percentage thresholds of habitat change increase, survey cessation (habitat change) rates for both BBS and the random model decline, which suggests a relatively high proportion of habitat change is less likely to be related to a survey cessation than a habitat change of low proportion (Figure 2 & S1). Although sample sizes for the higher proportions of habitat change are small and higher percentage thresholds of habitat change within a year are experienced less frequently, the overall rate of survey cessation (habitat change) decreased as the severity of habitat change increased: 14% of routes experiencing a year with habitat change ≥5% and <10% also experienced a cessation of recording, with only 2.5% of routes experiencing ≥30% habitat loss undergoing cessation (Figure 2-1&16). This may be due to the use of a relatively large study neighbourhood for each survey route (Figure S2, approximately 300 km^2), so that even a small proportion of habitat change may represent a major habitat change along the survey route. For example, most habitat changes constitute less than 15% of the total neighbourhood (Figure S2), and 15% increase of a habitat type would result in the change of about 45 km^2 of the surrounding habitats. At the same time, the BBS survey was conducted based on routes randomly located across the continent, whilst landscape transformation to anthropogenic habitats (e.g., road expansion, commercial and residential development) by definition occurs in relatively pristine areas; this may lead to critical effects on a survey, but usually does not account for a large proportion of the whole area (Figure S4) at this scale [12]. However, due to the relatively small sample size at more than 25% habitat change, how larger habitat change influence survey continuity needs more exploration.

We compared the trends of taxonomic diversity (TD), functional diversity (FD) and phylogenetic diversity (PD) for BBS routes with and without habitat change (Figure 3 & S3). In routes with no habitat loss, diversity metrics mostly increased over the sample period. This is likely caused by the rapid increase in biotic homogenisation at these less disturbed areas, which may lead to a global loss of species but no change or even an increase in local-scale diversity [6, 13]. However, diversity mostly decreased in routes with habitat change (Figure 3). The general result agrees with global-scale analysis by Jung et al. [7], who demonstrated from analysis of species occurrence and land cover data that abrupt habitat change was associated with local taxonomic diversity loss. That surveys tended to cease under the conditions that were associated with reductions in biodiversity suggests that the estimation of biodiversity change using longitudinal biological monitoring data may be incomplete and biased if it ignores the potential for non-random sampling.

Estimation of the size of this effect is not straightforward. Biodiversity change in survey cessation (habitat change) and survey continued (habitat change) routes might be very different, and simply inferring change in the former by the pattern of change documented in the latter may be misleading. Here we estimated the overall biodiversity trends had those routes where data collection stopped been included. We simulated diversity changes in survey ceased (habitat change) routes as different percentages of each route's diversity before cessation (Figure 4). Diversity in the subset of routes excluding survey ceased (habitat change) routes increased continuously to the mid-2000s, followed by a decrease (Figure 4-B, C & D), which is in accord with previous investigation of the temporal trends of North American bird diversity [4]. If survey ceased (habitat change) routes had been included, the overall diversity trend can be inverted from the observed growth to a decline depending on the extent of diversity loss in such routes. Specifically, the trend calculated by comparing diversity between the extreme 2001 and 2018 periods reversed if we assumed a quarter of diversity was lost in survey ceased (habitat change) routes, which account for 11% of the sampled routes in our study (Figure 4-A). The assumed diversity loss for an inverted trend decreased as the proportion of ceased (habitat change) routes increased, whilst a more negative diversity trend was found if there was diversity loss in survey ceased (habitat change) routes and their proportion increased (Figure 4-A). Our results indicate that biases in the collection of longitudinal data induced by non-random changes in sampling have the potential to significantly influence the estimation of overall biodiversity trends and highlight the magnitude of error that may be introduced when ignoring cessation bias.

Studies suggesting an absence of ubiquitous local species richness declines have been criticized for lack of baselines or reference conditions, variation in observers and their abilities, and for not using sufficiently long time series to achieve reliable conclusions [14-17], although some analyses have suggested these potential weaknesses did not influence the conclusion that there has been no decline [6, 18]. In this study we draw attention to a different problem: the potential that non-random data gaps in biological monitoring programmes, that might be caused by habitat change, may induce bias in estimating diversity trends. To exclude the effects of large data gaps, we only accounted for survey cessations that did not resume by the end of the study period, whereas a survey route that experienced a habitat-change induced stop may also later restart. This might be the case if habitat transformation occurs between natural habitats, or if a decision is made to sample secondary or successional habitats after disturbance. The overall rate of survey cessation (habitat change) may therefore be higher than we estimated here. Further studies quantifying biodiversity trends and the impacts of habitat change globally could benefit from distinguishing survey cessation with habitat change and survey cessation caused by other factors. A further issue, which we have not addressed here, is the possibility for positive reinforcement to create an additional bias. For example, if volunteers collecting survey data are more likely to persist in longitudinal surveys when local diversity trends are positive, this may lead to a further bias in longitudinal data, that would further mask larger-scale trends. The interaction between biodiversity and the behaviour of those collecting data on biodiversity is an under-studied area, worth further research.

Effects of changes of different habitat types on biodiversity are different [19]. Here, we focused on the change of the composition of different habitat types and did not differentiate between natural habitat losses and gains. We found no obvious trend for a certain habitat change type to be associated with survey cessation at less than 20% habitat change, whilst habitat change types that have higher probability to induce survey cessations at more than 20% habitat change are all between natural habitats or natural habitat mixed with croplands (Figure S4). This indicates that both gains and losses in natural habitat could cause survey cessations with no obvious difference at lower habitat change rates. Change between natural habitats could also induce survey cessations, e.g., the replacement of woodland by grassland could be regarded by a surveyor as no longer constituting a useful comparative time series. Although both changes of natural and anthropogenic habitats could cause a reduction in biodiversity [7] and survey cessations, diversity after different types of habitat change and their impacts on the estimation of biodiversity trend might be different. We propose further studies distinguishing the impacts of natural and anthropogenic habitat changes and exploring whether different drivers of habitat change, such as agricultural conversion, urban expansion or natural fires, have different impacts on the biodiversity trend estimation.

Evaluating biodiversity trends is of great importance [1]. Considerable debate on the generality of biodiversity trends across the globe has recently arisen due to divergent conclusions derived from two distinct approaches to estimating those trends [1, 20]. One is spatial comparisons by which measures of diversity in sites that are disturbed by human activities are compared to those in undisturbed reference sites. Such spatial comparisons often show global biodiversity is declining [21, 22]. The other is analysis of time-series data that have been collated from studies using repeated measurements of biodiversity at individual locations around the planet, which sometimes show global biodiversity is not declining [6, 13, 23]. Since the time-series datasets are distributed across different locations and over multiple geographic structures, the proliferation of such datasets and sometimes unexpected results have received considerable attention. Here, based on time-series data of a long-term biological monitoring programme, we show that the continuity of a biodiversity survey is more likely to be interrupted when major habitat changes occur, and that the major habitat change often leads to the reduction of biodiversity. Therefore, potential bias exists in the estimation of biodiversity using time-series data; the likely effect is that biodiversity loss is underestimated. We suggest researchers and conservation practitioners be aware of the potential bias, and call for strategies, tools and frameworks to continue to monitor the biodiversity change of major habitat change in future.

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AUTHOR CONTRIBUTIONS

W.Z. and K.J.G. conceived the ideas and all authors contributed critically to the methodology design. W.Z. performed the analyses and led the writing of the manuscript. All authors contributed to drafts of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Figure 1. Schematic illustration of potential sequences of survey cessation and habitat change. A. The survey cessation occurs one-year in advance or in the same year as the major habitat change. **B.** A one-year delayed survey cessation after the major habitat change. **C.** The survey ceased without being associated with habitat change. **D.** The survey continued despite habitat change. **E.** Survey continued without any habitat change. Note: survey data might contain random missing years but only those surveys that ceased and did not resume by the end of the study period are defined as ceased surveys in this study.

Figure 2. Frequency distribution of habitat change on survey routes. Density distribution of survey ceased (habitat change) rate for randomised habitat change (purple density plot) and the real habitat change (solid line) across different habitat change proportions and different cases. The survey ceased (habitat change) rate is calculated as the percentage of the number of survey ceased (habitat change) routes to total number of routes with habitat change. Numbers above each panel denote the number of survey ceased (habitat change) routes and percentages on the right-hand side denote the habitat change categories. See Figure S2 for route distribution and summary.

Figure 3. Temporal changes of taxonomic, functional and phylogenetic diversity in survey continued routes. Nonlinear regressions (a loess sliding window with a 33% range width; solid line) of different diversity facets were used to describe the major temporal trajectories across multiple habitat change categories. All diversity values were scaled from 0 to 1. Colour bands denote 95% confidence intervals. Number within the brackets is the sample size of that category. See Figure S3 for diversity comparisons between the beginning and the end of study period and also Figure S4 for summary on proportions of habitat change types.

Figure 4. Temporal changes of taxonomic, functional and phylogenetic diversity under assumptions that diversity in survey ceased (habitat change) routes reduced to different percentages of their diversity before cessation. **A.** The effects of survey ceased (habitat change) route proportion and their relative diversity loss on estimation of diversity trends. Relative diversity changes were compared between 2001-2003 and 2016-2018 periods assuming different percentages of diversity loss in survey ceased (habitat change) routes and different percentages of surveys ceased (habitat change routes) from the total numbers sampled. **B-D.** Temporal trends in three facets of biodiversity from 2001 to 2018. All diversity values were scaled from 0 to 1. The solid lines represent the smoothed spline (a loess sliding window with a 33% range width) with different colours indicating diversity loss in survey ceased (habitat change) routes of different percentages and colour bands denote 95% confidence intervals.

STAR★Methods

Resource availability

Lead Contact

Further information for resources should be directed and will be fulfilled by the Lead Contact, Wenyuan Zhang (wenyuan.zhang@zoo.ox.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and Code Availability

This paper analyses existing, publicly available data. These accession numbers for the datasets are listed in the key resources table. R code for performing our analyses is available at GitHub (https://github.com/plmyann/biotrends). Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

Experimental model and subject details

We used the North American Breeding Bird Survey data (BBS) to explore the effects of habitat change on the surveys of biological monitoring programmes, and subsequent estimation of biodiversity trends. The BBS is a long-term avian monitoring program which tracks the population dynamics of breeding birds and follows a strict survey protocol [3]. BBS data are collected once per year in June over 5000 survey routes that are located across North America. Each survey route is approximately 40km long. Routes are divided into 5 segments, each of ten stops at evenly spaced 800m intervals, giving 50 stops for each survey route. At each stop, trained observers record the birds that are seen or heard within a 400 m radius in 3 minutes. No new data was collected for this study and no physical experiments were conducted.

Method Details

Habitat Change Measure

We used a land cover product from the Terra and Aqua combined Moderate Resolution Imaging Spectroradiometer (MODIS), Land Cover Climate Modelling Grid (CMG) Version 6 (MCD12C1) [11] to estimate habitat change. There are 16 habitat types in MCD12C1 (under the International Geosphere-Biosphere Programme (IGBP) [26] land cover classification scheme): evergreen needle-leaf forests, evergreen broadleaf forests, deciduous broadleaf forests, mixed forests, closed shrub-lands, open shrub-lands, woody savannas, savannas, grasslands, permanent wetlands, croplands, urban and built-up lands, cropland/natural vegetation mosaics, permanent snow and ice, barren and water bodies.

MCD12C1 habitat types were used for the analysis mainly because of their relatively coarse spatial resolution and large temporal range. The spatial resolution of MCD12C1 is 0.05° (approximately 5km), which compared to the length of the routes (approximately 40km), can both detect the major habitat changes along a BBS route and exclude the noise of minor habitat changes. The classification schemes of MCD12C1 were provided at yearly intervals across the entire globe from 2001 to 2018. Since the BBS route protocol did not change over this period [3], we were able to use all routes with BBS records during this period giving a total number of 3014 routes (Figure S2A). A 5-km buffer was generated along each route, whilst the habitat change along each route was calculated by

$$\Delta H_{i,j} = \left|H_{i,j} - H_{i,j-1}\right|,$$

where $\Delta H_{i,j}$ is the absolute composition difference for habitat type i in year j, $H_{i,j}$ is the habitat composition for habitat type i in year j and $H_{i,j-1}$ is the habitat composition for habitat type i in year $j-1$. A binary habitat change index was created to indicate whether the largest change of the habitat types is for multiple magnitudes: ≥5% and < 10%, ≥10% and < 15%, ≥15% and <20%, ≥20% and < 25%, ≥25% and <30%, and ≥30% of the total buffer area, respectively.

To calculate whether changes of a particular habitat type are more likely to be associated with survey cessations, we estimated the cessation probability by comparing the frequency of a given habitat change type being associated with survey cessations with the frequency of that habitat change type among all habitat change types. We first classified the habitats into two categories: habitats transferring to others as donor habitats, and the habitats being transferred as recipient habitats. To measure the probability of survey cessations by a specific habitat transferring to other habitats, we defined a cessation probability for a given habitat change proportion k by

$$CP_{i,k} = \frac{n_{i,k}/n_k}{N_{i,k}/N_k},$$

where $CP_{i,k}$ is the cessation probability for a donor or recipient habitat type i, $n_{i,k}$ is the number of survey ceased (habitat change) routes by habitat type i, n_k is the total number of survey ceased (habitat change) routes, $N_{i,k}$ is the number of routes with habitat change in habitat type i, and N_k is the total number of routes with habitat change. $CP_{i,k}$ approaches 0 for minimum cessation probability and increases more than 1 for higher probability.

Survey Cessation with Habitat Change

The trained recorders of the BBS were expected to record the same route for long periods of time. However, reasons that lead to an interruption of a biological survey can be varied and include age, illness, loss of interest and so forth of the surveyors [27]. Surveys that ceased by these factors might restart if another surveyor was assigned to the previous survey route. However, cessations likely caused by habitat change are more difficult to restart for the survey routes can be lost. To distinguish cessations caused by habitat change and other factors, we defined habitat-driven survey cessation as having occurred when a survey stopped and did not restart by the end of the study period (i.e., 2018). This includes three scenarios. First, habitat change may have occurred since the preceding year's survey, leading to a decision to cease a scheduled survey before it was done. Second, the prospective recorder might have observed a major habitat change when they got to the survey sites and stopped the survey. Third, surveyors might have observed a habitat change while conducting the survey and then stopped it in the following year. The first and second scenarios cannot easily be distinguished through survey records since they both show a habitat change with a survey blank in the corresponding year. Therefore, we defined the first two scenarios as immediate survey cessation and the third as later cessation. For both the immediate and later survey cessation, the survey ceased (habitat change) rate for a given proportion of habitat change (k) was calculated by $R_{HCS,k} = \frac{n_k}{N_k} \times 100\%$, where R_{HCS} is the survey ceased (habitat change) rate for habitat change by proportion k, n_k is the number of routes with survey ceased (habitat change) by proportion k and N_k is the number of route with habitat change by proportion k.

We also built a null spatial model to investigate the effects of survey cessation (habitat change) by randomising the habitat change indices. Specifically, we first randomly distributed the 54108 binary habitat change indices across 3014 routes from 2001-2018, holding everything else constant, and calculated the rate of survey cessations (habitat change) with randomised habitat indices for both the immediate and later cessation. The relative survey ceased (habitat change) rate for a given proportion of habitat change (k) was calculated by $RR_{HCS,k} = \frac{sR_{HCS,k}}{rR_{HCS,k}}$, where sR_k is the actual proportion of routes with habitat change by k where surveying was ceased, and rR_k is the proportion of routes with randomly distributed habitat change by k where surveying was ceased. The procedure was replicated 1000 times.

Diversity Evaluation

To make comparison with recent studies on diversity trends [4, 13], we used encountered species richness (the sum of all species at a given BBS route) for taxonomic diversity (TD). Functional (FD) and phylogenetic diversity (PD) were also calculated without weighting for abundance. For the calculation of functional diversity, we used 16 traits from Elton Traits 1.0 [28]. These traits included: body mass, diet (i.e., proportional use of invertebrates, vertebrates, carrion, fresh fruits, nectar and pollen, seeds, and other plant materials in species' diet), foraging niche (i.e., prevalence of foraging below water surfaces, on water surface, on terrestrial ground level, in understory, in mid-canopy, in upper canopy, and aerial), and broad habitat types (i.e., pelagic or not), which are assumed to represent the Eltonian niche dimensions. We gave equal weights to each trait category, which resulted in 1 weight for body mass and broad habitat type and 1/7 for each diet and foraging niche variable. The functional distance was calculated using a multivariate trait dissimilarity under Gower's distance [29] for each pairwise species, followed by UPGMA clustering. Phylogenetic diversity was calculated using 100 dendrograms sampled from a full pseudo-posterior distribution of phylogenetic trees (http://birdtree.org). The mean phylogenetic diversity across these 100 dendrograms was calculated. For each route, FD was calculated as the total lengths of the functional dendrograms of the subtree joining the observed species on a route [30], and PD was calculated by summing up the total branch length of a sub-phylogenetic-tree joining the observed species on a route via root [31].

We calculated overall diversity trends in two ways: the yearly change of taxonomic, functional and phylogenetic diversity between 2001-2018, and a comparison of the two extreme 3-year periods, 2001-03 and 2016-18. For the first approach, we evaluated the temporal trends in all annual metrics using general additive models (GAMs). All diversity values were scaled from 0 to 1. To account for a difference in overall diversity level among routes, we included a random effect on BBS routes. For each model, we used a loess sliding window with a 33% range width. For the second approach, we lumped 3 years to avoid the potential effect of unusual or abnormal years. We retained routes surveyed in both periods for either approach to estimate the biodiversity trend. Then for the average diversity in the 2001 and 2016 periods, the relative diversity change - $\Delta D_{2001,2016}$ - for TD, FD and PD were computed respectively by $\Delta D_{2001,2016} = \frac{D_{2016} - D_{2001}}{D_{2001}} \times 100\%$.

We estimated effects of habitat change on biodiversity by comparing diversity trends in survey continued (habitat change) routes and survey continued (no habitat change) routes. To assess the magnitude of false biodiversity trend estimation likely caused by failing to record the biodiversity loss, we simulated the diversity loss in survey ceased (habitat change) routes as different percentages of their diversity before cessation. We also simulated different percentages of survey ceased (habitat change) routes compared with the total sampled routes to quantify the extent of the potential bias. For diversity change after the assumed diversity loss, we calculated an annually relative diversity change rate in survey continued routes to simulate diversity change in survey ceased (habitat change) routes. Specifically, for each pair of consecutive year m and n in survey continued years, we calculated the estimates diversity as $\Delta D_{m,n} = \frac{D_n - D_m}{D_m} \times 100\%$.

Quantification and statistical analysis

All statistical analyses are performed using R 4.0.0. Statistical details related to habitat change and association with survey cessations can be found in Method details. Diversity trends are estimated by fitting general additive models (GAMs) and comparisons between the beginning and end of the study periods, and details can be found in Diversity Evaluation from the Method details. Values are reported as mean value with 95% confidential intervals.

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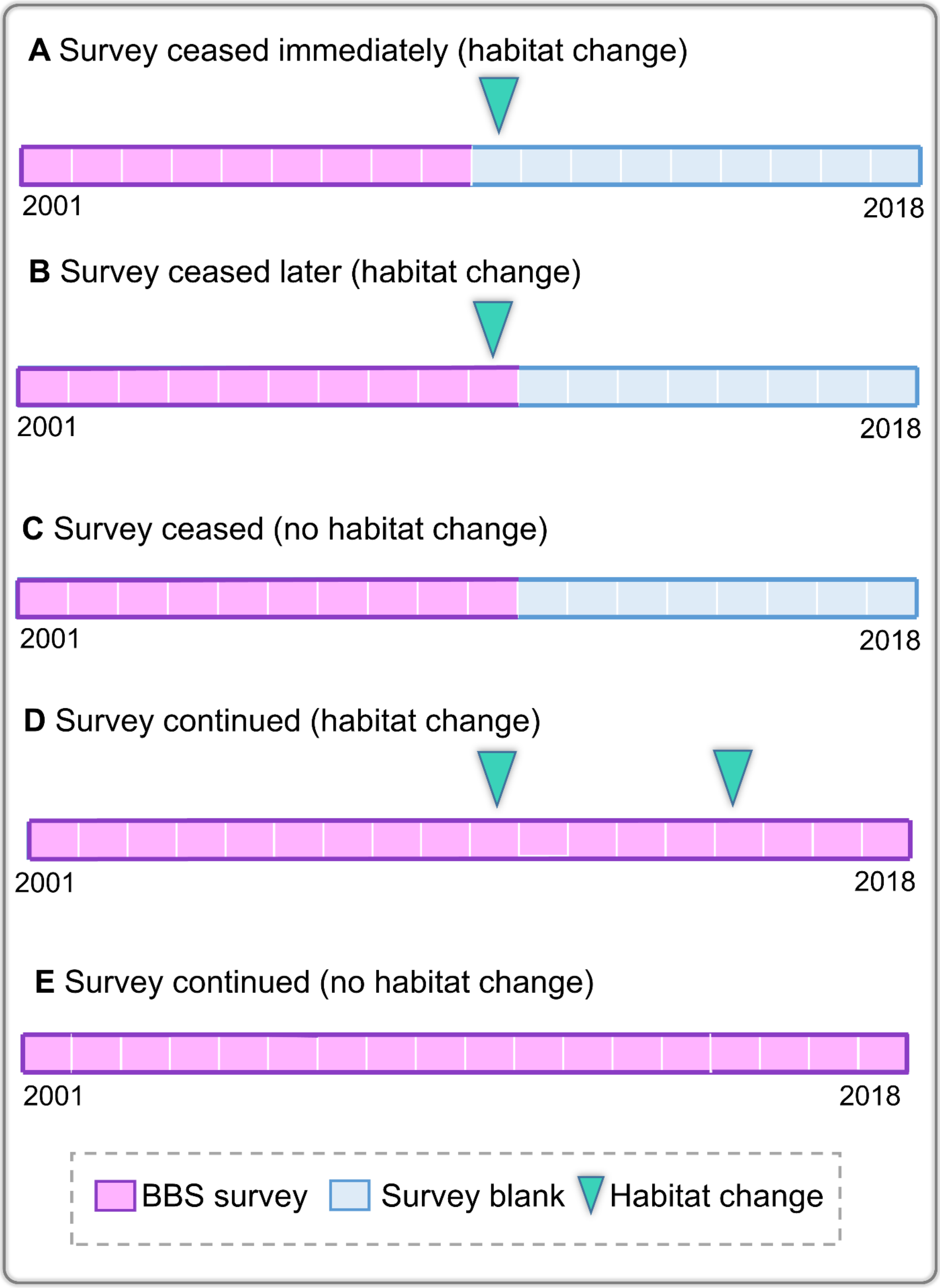
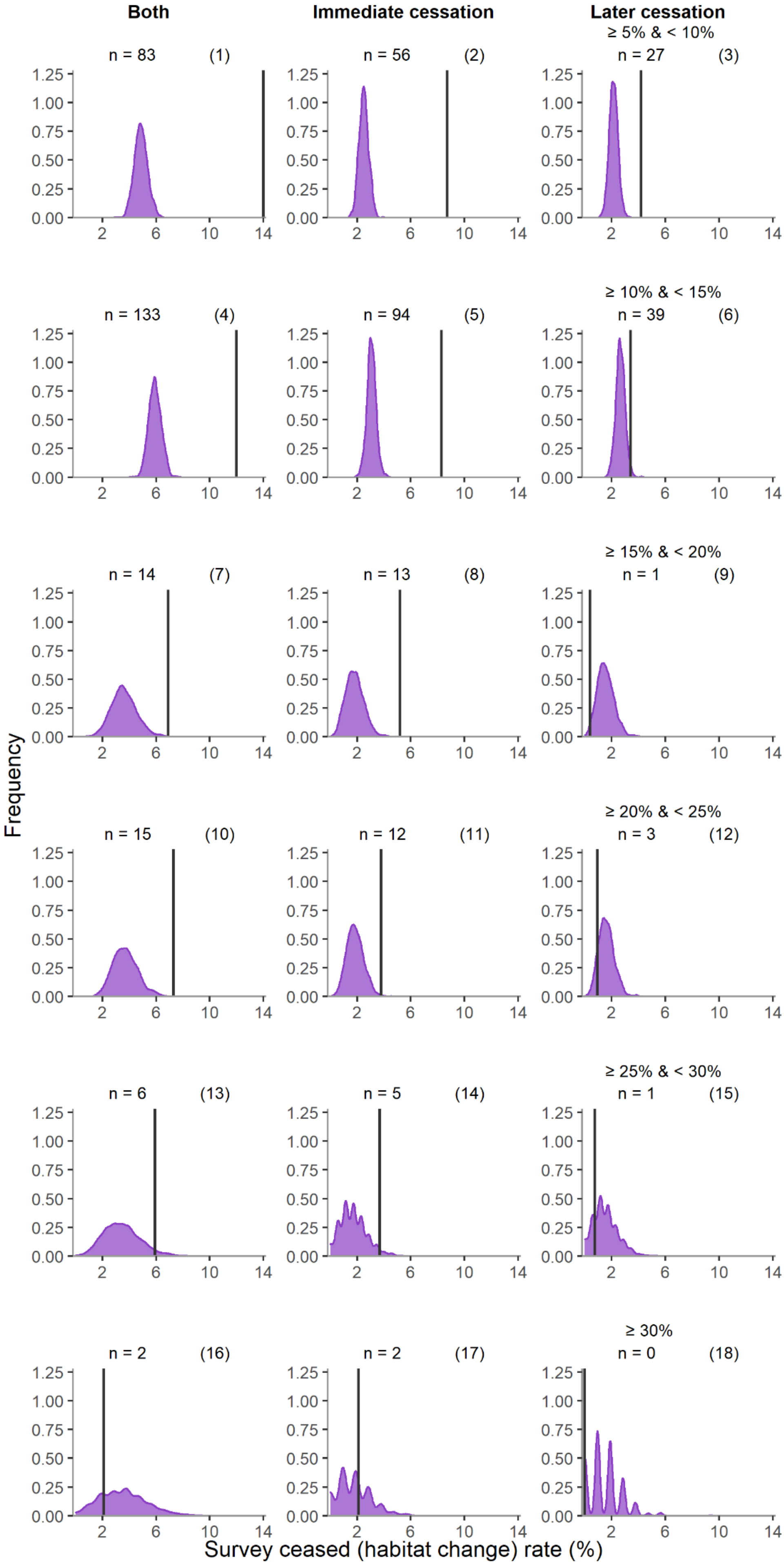
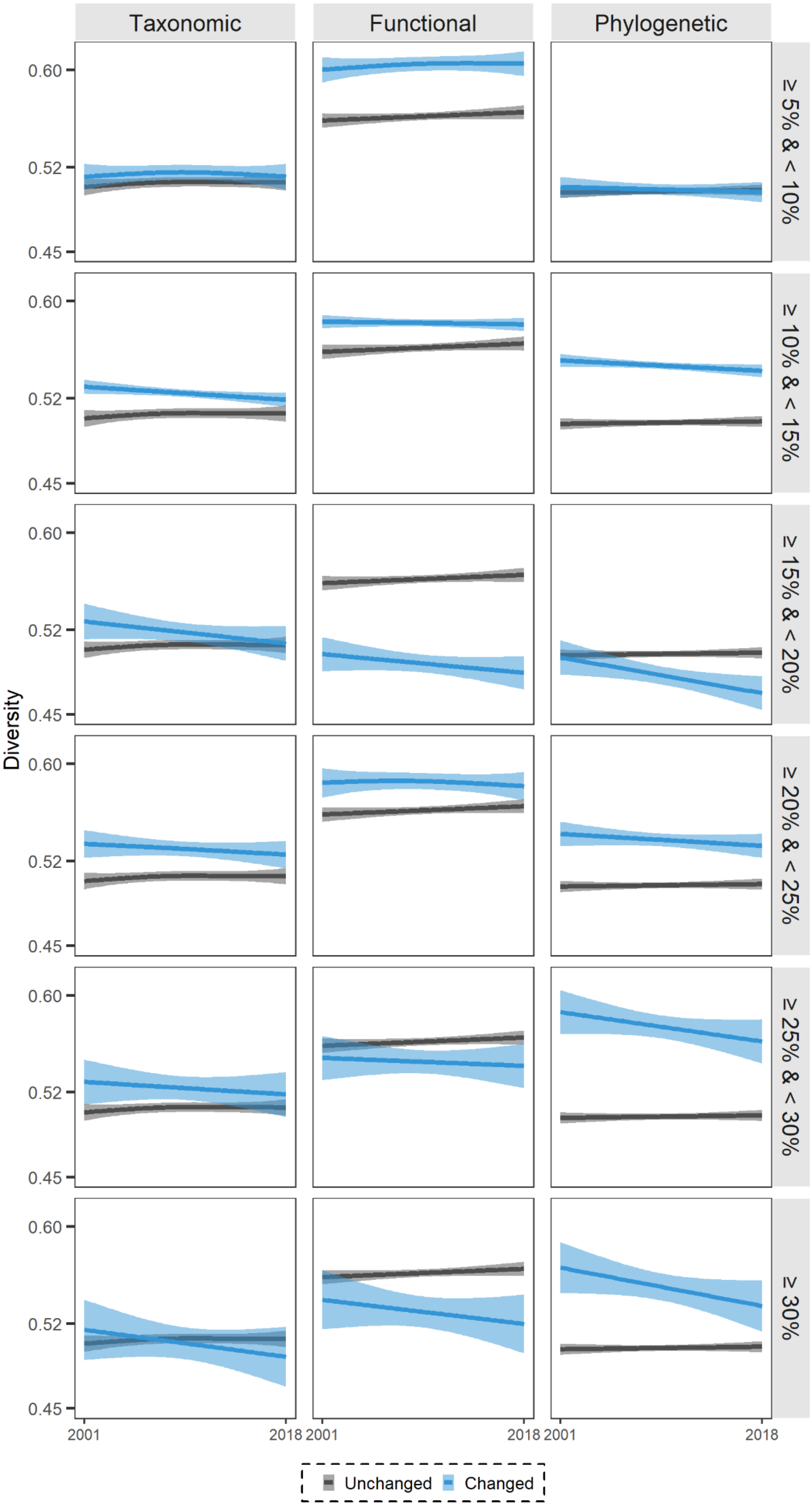

A Survey ceased immediately (habitat change)
2001
2018
B Survey ceased later (habitat change)
2001
2018
C Survey ceased (no habitat change)
2001
2018
D Survey continued (habitat change)
2001
2018
E Survey continued (no habitat change)
2001
2018
BBS survey
Survey blank
Habitat change



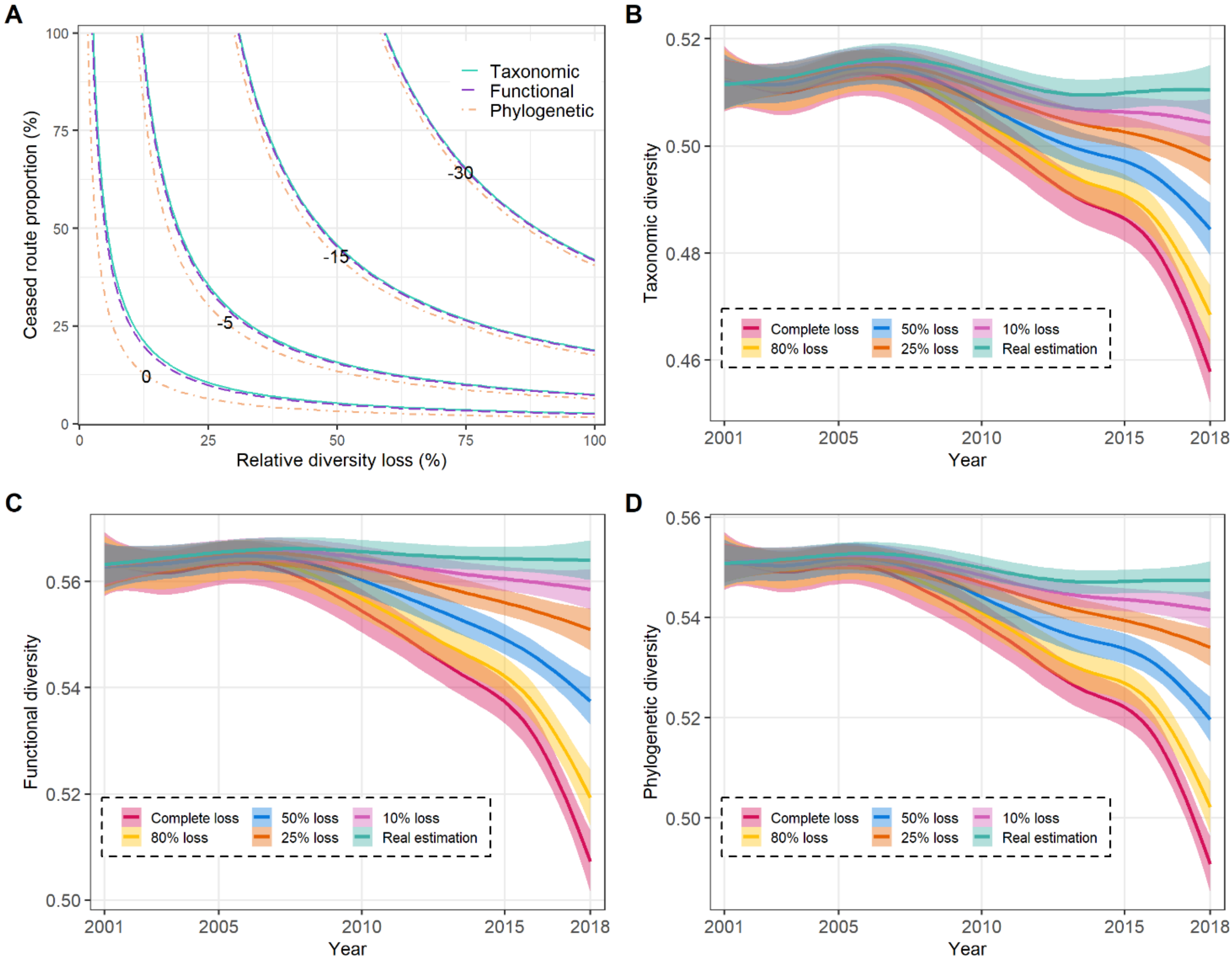
Both
Immediate cessation
Later cessation
≥ 5% & < 10%
n = 83
(1)
n = 56
(2)
n = 27
(3)
n = 133
(4)
n = 94
(5)
≥ 10% & < 15%
n = 39
(6)
n = 14
(7)
n = 13
(8)
≥ 15% & < 20%
n = 1
(9)
n = 15
(10)
n = 12
(11)
≥ 20% & < 25%
n = 3
(12)
n = 6
(13)
n = 5
(14)
≥ 25% & < 30%
n = 1
(15)
n = 2
(16)
n = 2
(17)
≥ 30%
n = 0
(18)
Frequency
Survey ceased (habitat change) rate (%)

508



Taxonomic
Functional
Phylogenetic
≥ 5% & < 10%
≥ 10% & < 15%
≥ 15% & < 20%
≥ 20% & < 25%
≥ 25% & < 30%
≥ 30%
Diversity
0.60
0.52
0.45
2001
2018
Unchanged
Changed

509


A
Taxonomic
Functional
Phylogenetic
-30
-15
-5
0
Ceased route proportion (%)
Relative diversity loss (%)
B
Taxonomic diversity
Year
Complete loss
80% loss
50% loss
25% loss
10% loss
Real estimation
C
Functional diversity
Year
D
Phylogenetic diversity
Year

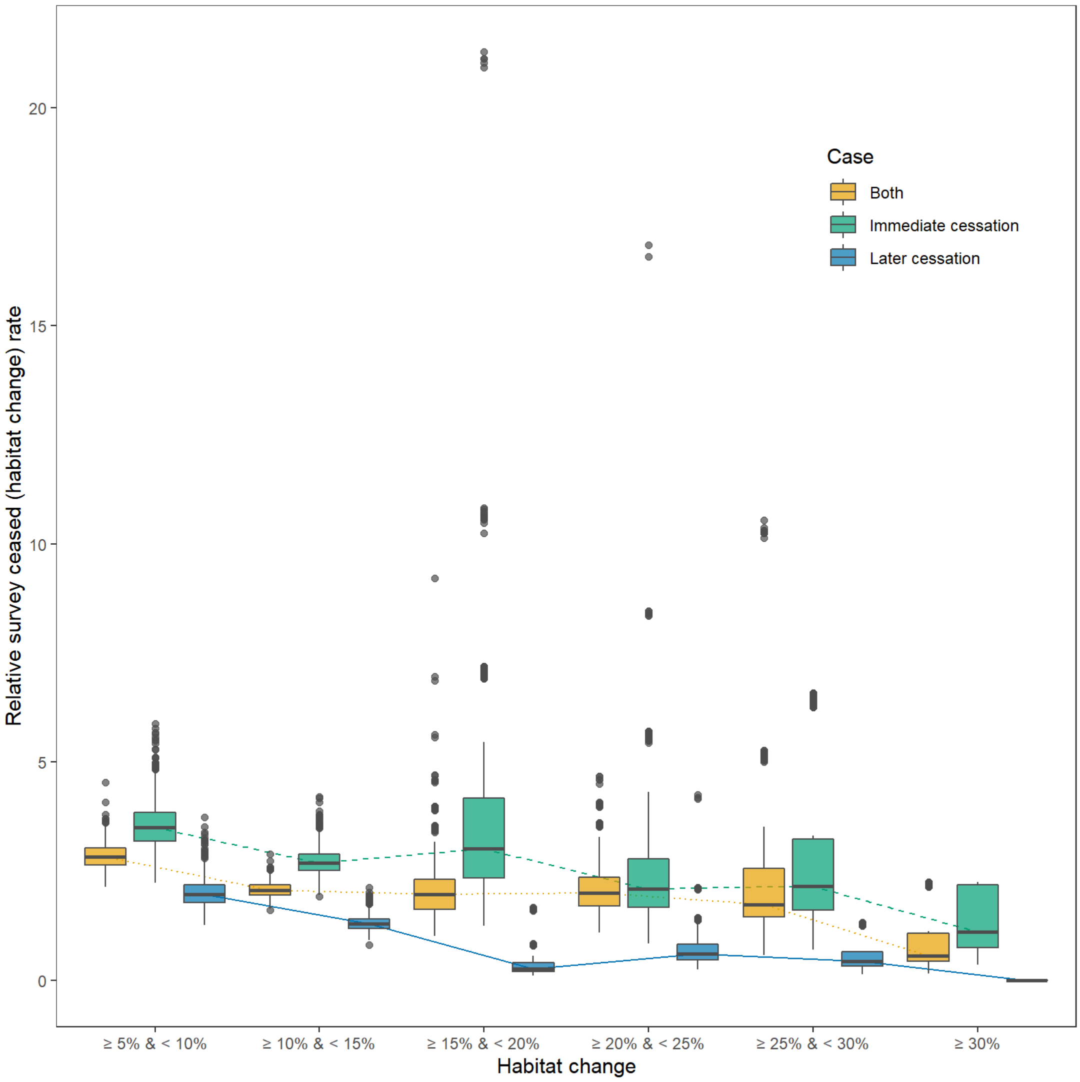


Figure S1. Change of the relative survey ceased (habitat change) rates in both immediate and later survey cessation routes for habitat changes of multiple categories. Related to Figure 2. The relative survey ceased (habitat change) rate for a given proportion of habitat change (k) is calculated by $RR_{HCS,k} = \frac{sR_{HCS,k}}{rR_{HCS,k}}$, where sR_k is the actual proportion of routes with habitat change above k where surveying was ceased, and rR_k is the proportion of routes with randomly distributed habitat change above k where surveying was ceased. The randomised procedure was replicated 1000 times. Boxes represent the 25th and 75th percentiles, lines within the boxes represent the 50th percentile (median), and whiskers represent 2.5th and 97.5th

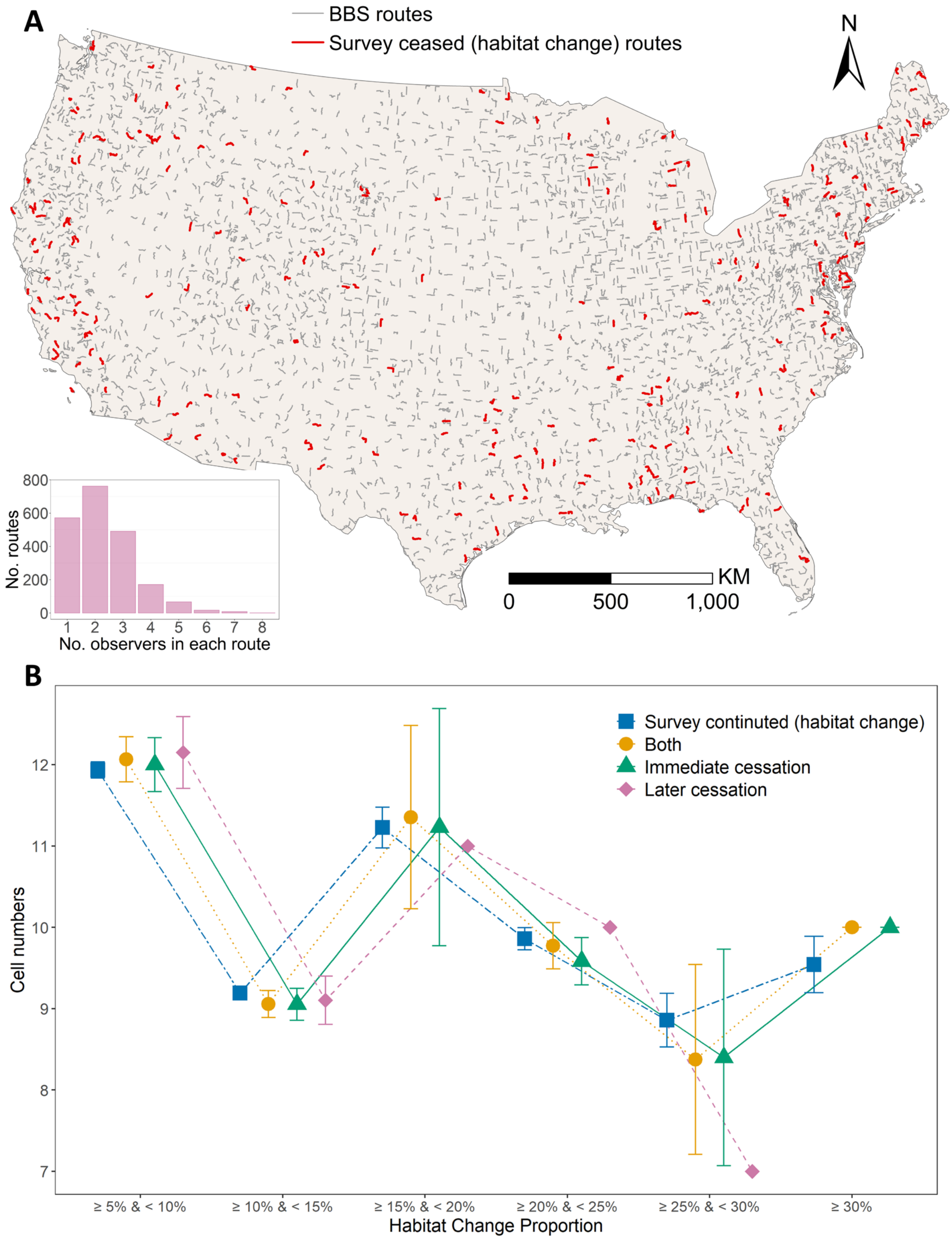


Figure S2. The distribution and summary of the survey routes in North American Breeding Survey programme. Related to Figure 2 and STAR Methods. A. BBS routes are the whole 3014 routes and survey ceased (habitat change) routes are the routes of habitat change over 5% around their neighbourhood and associated with survey cessations. The inset plot denotes the number of routes with different numbers of observers. **B.** Area of the neighbourhood around each route in different habitat change proportion presented by cell numbers extracted from the land cover map within 5-km buffer**.** The points represent the mean value of the relative diversity change and error bars represents 95% CI.

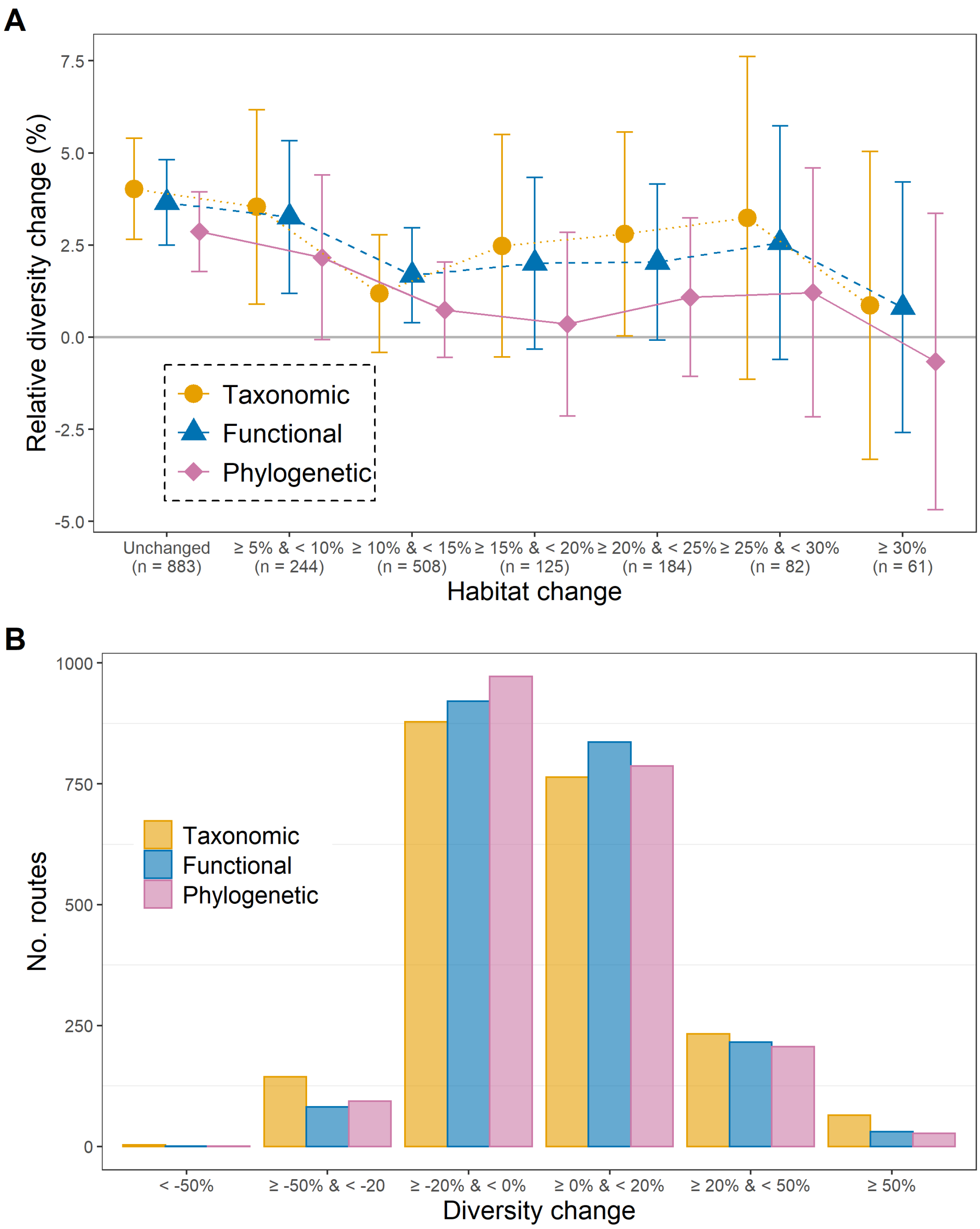


Figure S3. Diversity changes. Related to Figure 3. A. Relative diversity changes between 2001-2003 and 2016-2018 for routes without habitat change and routes with habitat change estimated at 5% - 10%, 10% - 15%, 15% - 20%, 20% - 25%, 25% - 30% and more than 30%. The points represent the mean value of the relative diversity change and error bars represents 95% CI. **B.** Number of survey continued routes with relative diversity change at less than -50%, -50% - -20%, -20% - 0%, 0% - 20%, 20% - 50% and more than 50%. Different colours denote different diversity forms.

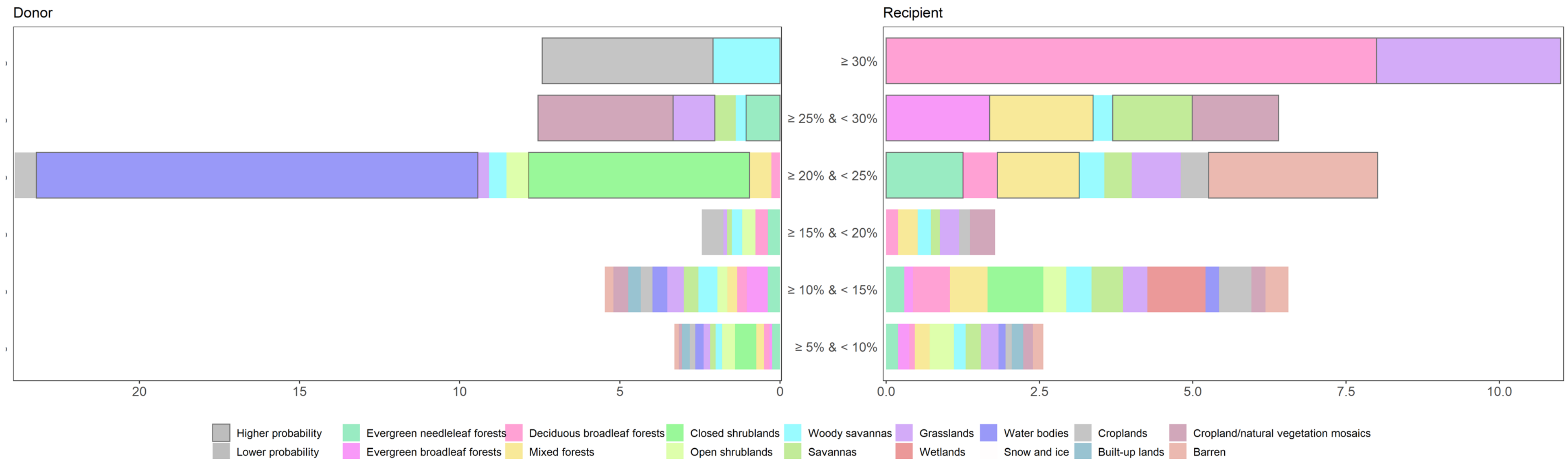


Figure S4. Proportions of habitat change types. Related to Figure 3. Donor means habitat loss and recipient means habitat increase. The bar denotes probability for a given a habitat type that likely caused survey cessation for a given habitat change proportion k, calculated by $CP_{i,k} = \frac{n_{i,k}/n_k}{N_{i,k}/N_k}$, where $CP_{i,k}$ is the ceased probability for a donor or recipient habitat type i, $n_{i,k}$ is the number of survey ceased (habitat change) routes by habitat type i, n_k is the total number of survey ceased (habitat change) routes, $N_{i,k}$ is the number of routes with habitat change in habitat type i, and N_k is the total number of routes with habitat change. $CP_{i,k}$ approaches 0 for minimum probability and increases more than 1 for higher probability. Different colours represent different habitat types.