Changes in the Biodiversity Intactness Index in tropical and subtropical forest biomes, 2001-2012

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Abstract

Few biodiversity indicators are available that reflect broad-sense biodiversity - rather than particular taxa - at fine spatial and temporal resolution. The Biodiversity Intactness Index (BII) reports how the average abundance of native terrestrial species in a region compares with their abundances before pronounced human impacts. BII is designed for use with data from a wide range of taxa and functional groups and for estimation at any resolution for which data on land use and related pressures are available. For each year from 2001 to 2012 we combined models of how land use and related pressures in tropical and subtropical forested biomes affect overall abundance and compositional similarity with data on anthropogenic pressures. We used these data to produce annual maps of modelled BII at a spatial resolution of 30 arc seconds (roughly 1km at the equator) across tropical and subtropical forested biomes. This is the first time temporal change in BII has been estimated across such a large region. The modelling approach used for compositional similarity is an improvement over that used previously when estimating BII, using data more efficiently. Overall, BII fell by an average of 2.4 percentage points between 2001 and 2012, with 83 countries seeing an average reduction and 45 an average increase, and the extent of primary forest fell by 3.9% over the same period. Changes are not strongly related to countries' rates of economic growth over the same period.

Keywords: land-use change; biodiversity indicators; PREDICTS; IPBES.

Introduction

Biodiversity indicators can play an essential role in tracking progress towards policy targets, especially if the indicators link strongly to both the targets and biodiversity, have broad geographic coverage, and are available as a time series (Tittensor et al. 2014). These stringent criteria have contributed to a strong taxonomic bias in biodiversity indicators (Dobson 2005; Walpole et al. 2009; Butchart et al. 2010; Tittensor et al. 2014). In an assessment of whether the rate of biodiversity loss had fallen by 2010 (Butchart et al. 2010), only one of four indicators of the state of biodiversity considered any non-vertebrate data (the Red List Index considered corals in addition to birds, mammals and amphibians) and none of the three measures of benefits accrued from biodiversity did so. The bias is if anything stronger among indicators considered in a mid-term analysis of progress towards

the Aichi 2020 Targets (Tittensor et al. 2014): only one of the nine measures of the state of biodiversity (coral reef cover) considered non-vertebrate data, and none of the three measures of benefits did so. Indicators based on a taxonomically-broad sets of species are urgently needed (Jones et al. 2011) because species in different clades often respond differently to given pressures (e.g., Lawton et al. 1998; McKinney 1997; Cardillo et al. 2008; Newbold et al. 2014).

In addition to taxonomic bias, available biodiversity data show strong geographical biases. Many tropical regions tend to be under-represented relative to well-recorded regions such as North America, Western Europe and Australia (McRae et al. 2017; Hortal et al. 2015; Meyer et al. 2016). This is for a range of socioeconomic reasons (Meyer et al. 2016). If locations are biased relative to the distribution of anthropogenic pressures, the average trend inferred from the data may not accurately reflect the true global trend (Gonzalez et al. 2016; Purvis et al. 2018) unless the bias is corrected for (e.g., McRae et al. 2017).

The Biodiversity Intactness Index (BII: Scholes & Biggs 2005) is designed to reflect the status of a much broader set of taxa than most other indicators. BII is defined as 'the average abundance of a large and diverse set of organisms in a given geographical area, relative to their reference populations' (Scholes & Biggs 2005). The reference condition is approximated as the contemporary situation in minimally-impacted sites, given the paucity of historical baseline data (Scholes & Biggs 2005). BII was estimated originally using expert judgement in lieu of detailed primary-biodiversity data (Scholes & Biggs 2005). More recently, Newbold et al. (2016a) estimated BII globally for the year 2005 by combining global maps of pressures with two statistical models (one of the effects of land use and related pressures on overall sampled organismal abundance; one of how land use affects compositional similarity to an assemblage in primary vegetation. Both models are described in more detail by Purvis et al. 2018). These statistical models were fitted to a global compilation of studies that had each conducted a comparable ecological survey at multiple sites facing different pressures (described in Hudson et al. 2014), with a total of 39,123 plant, fungal or animal species and 18,659 sites spanning all 14 of the world's terrestrial biomes (Newbold et al. 2016a). The models assumed that the relationships between pressures and biodiversity do not vary regionally, but the underlying database (Hudson et al. 2017) has now grown to the point that it can support some region- or biome-specific modelling. This is important given the likelihood of regional variation in responses (e.g., Gibson et al. 2011; De Palma et al. 2016; Newbold et al. 2016b; Phillips et al. 2017).

The global estimates for BII in the year 2005 made use of fine-scale (1km-resolution) maps of land use (Hoskins et al. 2016) produced through statistical downscaling of global 0.5-degree harmonized land-use data (Hurtt et al. 2011). Remote sensing has greatly improved the ability to track land-cover change at fine spatial and temporal resolutions (Pettorelli et al. 2016). Methods such as those developed by Hoskins et al (2016) have the potential to convert such data to time-varying land-use estimates, providing a time series of pressure data that can be combined with the statistical models that link pressures to biodiversity. This could help estimate BII annually and thereby greatly enhance its usefulness as an indicator. We focus here on forest biomes given that detection of forest loss is better developed than detection of grassland loss (Hansen et al. 2013).

Tropical and subtropical forest biomes cover about 17% of the globe's land surface but are home to most of the world's terrestrial species and the ecosystem services they provide sustain well over 1 billion people (Lewis et al. 2015). Land-use change is the major threat globally to tropical forest biodiversity (Sala et al. 2000) and is driven by a combination of factors that include agricultural expansion, timber extraction and infrastructure development (Geist & Lambin 2002), though rates and patterns of forest loss differ regionally (Lewis et al. 2015). Deforestation and degradation reduce local species-richness across a range of groups (Gibson et al. 2011; Newbold et al. 2014; Barlow et al. 2016) but no biodiversity indicators are yet available that give a taxonomically-broad picture of the status and trend of tropical forest biodiversity that is well resolved spatially and temporally. Here we use annual global fine-resolution maps of land use and human population density to map modelled BII across the world's tropical and subtropical forests for each year from 2001 to 2012. Summary statistics of average change in BII at national and regional levels will be relevant for biodiversity assessments such as those being undertaken by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the Group on Earth Observations (GEO).

Methods
1. Statistical models of how biodiversity responds to pressures

a. Biodiversity data
The models we use are adapted from Newbold et al. (2016a). Models are based on the PREDICTS database, a global collation of spatial comparisons. The database contains surveys ('studies') of multiple sites differing in land use and related pressures (Hudson et al. 2014; Hudson et al. 2017). The data were subset to only consider sites in the following tropical or subtropical forested biomes: tropical and subtropical coniferous forests, tropical and subtropical dry broadleaf forests and tropical and subtropical moist broadleaf forests. We only considered studies where communities were sampled, rather than studies that sampled only a single target species. The final dataset used for analyses contained 777,173 records from 180 published sources on the abundance of 20,740 species from 5159 sites worldwide (representing 45 countries). Invertebrates make up 42.9% of the species, plants 36%, vertebrates 18.7% and fungi 2.4%.

b. Pressure data
The PREDICTS database holds site-level data on land use (primary vegetation, secondary vegetation, plantation forest, cropland, pasture or urban) and land-use intensity (minimal, light and intense), classified using information in the original sources or information provided by their authors (see Hudson et al. 2014 for details). Although plantation forest exists as a separate land-use class in the PREDICTS database and is characterised by assemblages that are both relatively low in species richness and compositionally distinct (Newbold et al. 2015), it is rarely separated from other forests in global land-use layers; this is also true in this case. One option (used by Newbold et al. 2016a) is to model responses to plantation forest but omit the effect when projecting results across space. Given the importance of plantation forests in tropical forested areas, we chose instead to group plantation forests together with secondary vegetation when modelling. We did this because it is the most likely source of plantation forest in the global land-use layers and previous work (Gibson et al. 2011) has shown little difference between losses caused by primary conversion to secondary vegetation or plantation forest. In models where different land-use intensities can

be considered, lightly- and intensively-used plantation were included with intensively-used secondary vegetation, and minimally-used plantation was included with lightly-used secondary vegetation. In addition to land-use and intensity, we included other pressures; for the grid cell containing each of our sites, we extracted the human population density (for the year 2005 from CEISIN 2016) and the density of roads (derived from CEISIN 2013) at the 1km and 50km scales. Environmental conditions for each site were extracted from WorldClim (elevation, max temperature of the warmest month, min temperature of the coldest month, precipitation of the wettest and driest month; Hijmans et al. 2005).

c. Mixed-effects models

Two mixed-effects models (lme4 version 1.1-15, Bates et al. 2015) were then run. The first model focussed on total abundance, which was calculated as the sum of abundance across all species recorded at each site. If sampling effort varied within a study, abundance was rescaled assuming that diversity increased linearly with sampling effort. Within each study, total abundance was then rescaled so that the maximum value was unity; this rescaling reduces the inter-study variance caused by differences in sampling effort and taxonomic focus. Rescaled total abundance was square-root transformed prior to modelling, which used Gaussian errors (non-integer abundance data even before rescaling precluded modelling of untransformed data with Poisson errors, and square-root transformation resulted in a better residual distribution than ln-transformation). Rescaled total abundance was then modelled as a function of site-level land use and intensity (LUI), human population density (ln(x+1) transformed), and density of roads at the 1km and 50km scale (cube-root transformed), along with two-way interactions of LUI with each other pressure (as fixed effects). We included an additional control variable to account for among-study differences in human population density (by taking the mean value within each study); this was to control for potential sampling and detection biases where sampling may be more complete in areas of higher human population density (which are generally closer to research institutions and more accessible for sampling). All continuous variables were centered and scaled to reduce colinearity. We used a random-effect structure of block within study, to account for differences in sampling methodology and large-scale environmental differences across studies and the spatial structure of sites within studies. With the model fit using Restricted Maximum Likelihood (REML), we assessed whether random slopes were required by comparing Akaike's Information Criterion (AIC) for models with each variable fit as a random slope in turn. The best fixed-effects structure was then determined using backwards stepwise model simplification with the model fit using Maximum Likelihood (Crawley, 2007).

The second model assessed the response of compositional similarity to human impacts. We excluded studies where sampling effort varied among sites. For studies with at least one site classed as minimally-used primary vegetation (the baseline site), we calculated for each study in turn the compositional similarity of each site to assemblages in each baseline site, measured as the proportion of $site_j$'s individuals that belong to species also present in $site_i$ (where $site_i$ is in minimally-used primary vegetation, i.e., an asymmetric version of the abundance-based Jaccard similarity index: Chao et al. 2005; Newbold et al. 2016a). These pairwise differences were modelled using a mixed-effects framework. We again included as explanatory variables human population density and density of roads at 1km and 50km radius, transformed as before. Compositional similarity between any pair of sites will be influenced by how much more impacted one site is compared with the baseline, as well as the absolute level of pressure faced by the comparison site. For each continuous pressure

variable, we therefore include in the models both the value at site$_j$ as well as the difference in value between site$_i$ and site$_j$. We included geographic distance (ln-transformed) and environmental distance (Gower's 1971 dissimilarity calculated using the *gower* package in R, van der Loo, 2017, then cube-root transformed) between sites to account for decays in compositional similarity with distance (Newbold *et al*, 2016b). Geographic distance was divided by the mean maximum linear extent (sampling grain) in the dataset. The land-use contrast was included as a fixed effect along with its interaction with other continuous variables. As this dataset is more restricted than that used for abundance (because only studies that sample minimally-used primary vegetation can be used), we do not consider effects of use intensity within land uses, other than for primary vegetation (split into minimally-used primary vegetation and a combined class of lightly- and intensively-used primary vegetation). Finally, we included the mean value of human population density within each study as a control variable. Compositional similarity was logit transformed as data were bound between 0 and 1 (*car* package, version 2.1-6, Fox & Weisberg, 2011; an adjustment of 0.01 was used to account for values of 0 and 1). We included Study as a random intercept and assessed whether a random slope was supported by using the same framework as before, choosing the random structure with the lowest AIC value where the model was able to converge. Backwards stepwise model simplification was performed to simplify the fixed effects structure of the model fit using Maximum Likelihood. Traditional significance tests based on likelihood ratios are not accurate here, because the data used are not independent (as each site is compared to multiple other sites within the same study). We therefore used permutations to determine whether a variable could be excluded from the model without significant loss of explanatory power. We did this by permuting the dataset 1000 times by randomly shuffling compositional similarity measurements within each study and refitting both the full and simplified model with this dataset. We then compared the likelihood ratio of our observed models with the distribution of likelihood ratios for the 1000 permuted datasets to assess whether the ratio was significantly higher than expected based on models with the same differences in parameters. Note that this approach to modelling compositional similarity differs from that used by Newbold et al (2016a), where 100 models were run such that in any one model, sites were randomly chosen from the database so that each site is only compared with one other site; the coefficients are then averaged across the 100 models. Here, we use a matrix-based approach, using all relevant site comparisons in the same model, allowing us to make full use of the data; however, permutation tests are required to assess significance of variables and coefficients to account for pseudoreplication of data.

Diversity analyses were performed using *R* Statistical Software (version 3.4.3, R Core Team, 2017). Prior to modelling, all explanatory variables were assessed for multicolinearity using Generalized Variance Inflation Factors (GVIFs, Zuur et al. 2009) for each model; all values were below 5, indicating acceptable levels of colinearity.

2. Global pressure data and maps of BII for each year

a. Land use. Hoskins et al. (2016) statistically downscaled global land-use data for the year 2005 (Hurtt et al. 2011) from 0.5 degree resolution to 30 arc-second resolution. The data report the fraction of each pixel in each of the following classes: primary habitat, secondary habitat, cropland, pasture and urban. The approach was extended here, by integrating the data for 2005 with remotely-sensed data on land cover and forest change.

The original method described in Hoskins et al (2016) uses a combination of Generalised Additive Models (GAMs) and constrained optimisation to produce fine-grained predictions of multiple land-use classes. We made several modifications to the downscaling method in order to generate our land-use time-series. To improve predictions outside of the fitted parameter space, we performed AIC-based backwards stepwise model selection, to identify the most parsimonious set of predictor variables. We then fitted our downscaling models to the year 2005 coarse-grained Land-Use Harmonisation data (Hurtt et al. 2011) and, using time-varying covariates, used these models to predict land-use for the full time-series. Our time-varying covariates were derived from a land-cover product with a yearly temporal resolution (Freidl et al. 2010). Once our downscaling models were fitted to the 2005 data of this land-cover dataset, we were able to predict land-use change using the remaining years in the time-series.

We also maximised the influence of the time-varying covariates in our downscaling models by fitting the GAMs in two stages. Initially the GAMs were fitted to only the time-varying covariates (i.e. land cover change datasets), allowing these to explain as much variation in the data as possible. The static covariates were fitted only in a second step, so that they were only able to describe variation not already described by the time-varying covariates. This resulted in models that maximised information coming from the time-varying land-cover data and, as such, reflect the temporal change in the land-cover layers as much as possible in our land-use predictions.

Within tropical and sub-tropical forested regions (defined as Tropical and Subtropical Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests and Tropical and Subtropical Coniferous forests in Olson et al. 2001), we further refined our land-use estimates by integrating the Global Forest Changes (GFC) dataset (Hansen et al. 2013) using the following rules. Within a cell, when the predicted proportion of primary habitat was greater than observed by GFC, primary was reduced to match the GFC-observed forest cover. All other land-uses were then scaled proportionally to their predicted values to ensure all constraints were met. When the sum of predicted primary and secondary habitat were less than observed GFC data they were scaled proportionally so that their sum matched the GFC data. The remaining three land-uses were then scaled proportionally to ensure all constraints were met. This provided land-use estimates within forest biomes that were consistent with the observed change in the GFC dataset.

b. Human population density. We downloaded human population density data for the years 2000, 2005, 2010 and 2015 from http://beta.sedac.ciesin.columbia.edu/data/collection/gpw-v4 (adjusted to match 2015 revision of UN WPP Country Totals). After ln(x+1) transformation (the 1 is added to avoid problems caused by zeroes in the data), we interpolated data for intervening years by assuming linear change in ln(human population density + 1) over time. For example, a cell's value for 2006 is given by 0.8 * value for 2005 + 0.2 * value for 2010.

c. Density of roads. We used a vector map of the world's roads (CEISIN 2013) to derive maps of road density: for each 1km cell, road length is calculated within a 1km and 50km radius from the centre point of the cell and expressed as density per 1km cell of land (using the arcpy functions of LineLength and FocalStatistics (ArcGIS v10.5). In the absence of any

global time-series data of roads, we treated this layer as a static, rather than dynamic, pressure in our projections.

d. Land-use intensity. To estimate land-use intensity for each year, we applied Newbold et al.'s (2015) statistical models of land-use intensity to each year's data on land use and human population density and the (static) data on proximity to roads. Briefly, Newbold et al. (2015) reclassified the Global Land Systems dataset (van Asselen & Verburg 2013 GCB) into land-use/use-intensity combinations and then modelled how the proportional coverage of each combination within each 0.5 degree grid cell depended on the proportion of the grid cell under that land use, human population density and UN sub-region (and all two- and three-way interactions).

e. Maps of modelled BII for each year. We used each year's maps of land use, land-use intensity and human population density, along with the (static) maps of road density to drive the two statistical models of how biodiversity responds to pressures. For total abundance, the values were expressed relative to the baseline of minimally-used Primary vegetation with zero human population and road density. For compositional similarity, values were expressed relative to minimally-used Primary vegetation sites, with zero human population and road density and zero environmental distance and geographic distance (note that for the latter, this equates to the mean sampling grain in the dataset). Control variables were set to zero. Projections of abundance and compositional similarity were not allowed to exceed the predicted values observed in our models, to prevent extrapolating beyond the bounds of our data. Multiplying these spatial projections together produces BII. We did this for each year between 2001 and 2012. Average BII values for each country, subregion and region were calculated for each year by averaging modelled values across all grid cells intersecting the relevant region's shape file (as defined for the IPBES assessment, from Brooks et al. 2016) after re-projecting (Behrmann equal area projection). To assess overall trends across the time period, we calculated the log response ratio of start (year 2001) and final (year 2012) values as $ln\left(\frac{bii_{2012}}{bii_{2001}}\right)$. Wilcoxon signed rank tests were used to assess average trends across all countries. We also visually relate these changes to contemporaneous changes in GDP per capita (in current US dollars, World Data Bank).

Results

Total abundance was significantly influenced by interactions between land use and both human population density (x^2 = 22.23, df = 10, p < 0.05) and road density at the 50km^2 scale (x^2 = 25.10, df = 10, p < 0.01). For the model of compositional similarity, all terms were maintained during model simplification (each significant at the p < 0.01 level according to the permuted likelihood ratio tests).

On average across the tropical forested biomes, BII fell from 57.3% in 2001 to 54.9% in 2012 (Fig 1); a rate of loss of approximately 0.2% per year. All regions saw an average decline in BII over the period, with Asia and the Pacific suffering the greatest losses over this time period (-2.8 percentage points) and the least severe declines in Africa (-1.4 percentage points); similarly, Asia and the Pacific suffered the worst declines in primary vegetation (-2.3

percentage points), while Africa saw average increases, although minor (+0.6 percentage points).

Changes in BII from 2001 to 2012 varied among countries (Fig 2), ranging from increases of up to 8.8 percentage points to decreases of 14.5 percentage points. On average, the median log response ratio (-0.14) was significantly negative (V = 2547, *p*-value < 0.001). When considering only those countries where at least 50% of their area is included in the analysis (because they are within the tropical forest biomes), most countries showed average losses over the time period (Fig 2). Average change over time at the country level were not clearly related to changes in gross domestic product per capita (Fig 3 and Fig S2).

Discussion

Although human impacts on the rate of global species extinction have perhaps attracted more concern (Ceballos & Ehrlich 2002; Barnosky et al. 2011; Pimm et al. 2014), local diversity matters more than global diversity for reliable provision of many ecological functioning and services. Reduction in local diversity is associated with reduced rates of delivery of key functions (Hooper et al. 2012) as well as greater variance in those rates (Cardinale et al. 2012). This closer link is one reason why the Biodiversity Intactness Index (BII) was proposed as a metric that could be used to assess the state of biodiversity relative to its proposed planetary boundary (Mace et al. 2014; Steffen et al. 2015). In addition, losses across trophic groups can have larger impacts on ecosystem function than losses within a trophic group (Cardinale et al. 2012) so, by including multiple taxa, BII may be more functionally relevant than many other measures of local diversity.

BII is likely to be a useful indicator of the state of biodiversity in tropical forests, where single taxonomic groups can be inefficient indicators for the responses or diversity of other groups (Lawton et al. 1998; Kessler et al. 2009; although see Schulze et al. 2004). In addition, the computation of BII used here combines both alpha diversity (total abundance) and beta diversity (compositional similarity) to estimate the abundance of 'originally-present species'. These two aspects of diversity can show contrasting patterns (Mandl et al. 2010) and responses to human impacts (Socolar et al. 2016; Hillebrand et al. 2018). The contrast may in part help to explain the recent debate on how human impacts have been affecting the diversity of local ecological assemblages. Two meta-analyses of assemblage time series have reported no temporal trend in alpha diversity (Vellend et al. 2013; Dornelas et al. 2014), whereas analyses that substitute spatial comparisons for temporal comparisons suggest a slight but significant average reduction over time (Newbold et al. 2015; Murphy & Romanuk 2013).

Steffen et al. (2015) proposed a global 'safe limit' of biosphere integrity at 90%, with a lower bound of 30%. Although it is unclear whether such a threshold exists either globally or across particular biomes as analysed here, or what value this threshold takes (Brook et al. 2013, Mace et al. 2014), our results suggest that losses in BII had already far exceeded the proposed upper bound by 2001 with an average value of 57.3%. Such a low value is unsurprising, given that the highest rates of deforestation in tropical forests occurred during the 1980s and 1990s (Morris, 2010).

Within-country trends showed substantial variation over the time period, but most countries (and on average all but two subregions) showed declines. Only three countries have remained above the 90% BII threshold: French Guiana, Suriname and Papua New Guinea. This provides a worrying picture for the state of biodiversity in tropical and subtropical forests. Land-use conversion was of course an important predictor of biodiversity loss, but degradation at local (1km) and broader (50km) scales were also significant contributors. For primary vegetation, some of the strongest declines in compositional similarity were seen as road density increased at broader spatial scales, particularly in lightly and intensively-used primary vegetation. This suggests that we need to protect natural intact vegetation at varying spatial scales to conserve local diversity. Indeed, the amount of natural intact vegetation is low and continuing to decline (Sloan et al. 2014; Venter et al. 2016). However, despite the suggestion that forest loss and degradation tend to be concentrated in poorer countries (Sloan & Sayer, 2015), there was no clear pattern between trends in GDP per capita and BII trends over time (although there was some suggestion that, across countries, BII tended to be lower in 2012 in poorer countries, Appendix Figure S1).

We have so far only considered the impacts of land-use change and related pressures on biodiversity, which are the most important drivers of biodiversity loss in the recent past and future, particularly in the tropics (Jetz et al. 2007). However, climate change is likely to have an increasingly important impact over longer timescales, especially as forest conversion already leads to strong changes in local temperature, potentially exacerbating future impacts of climatic change (Senior et al. 2017). Incorporating both land-use change and climate change impacts could improve estimates of biodiversity change (de Chazal & Rounsevell 2009).

The average BII values reported here are substantially lower than the recently published global average, where BII across the terrestrial surface was found to be approximately 84.6% (Newbold et al 2016a). This discrepancy is likely due to a combination of: (1) new land-use maps that have stricter bounds on the extent of primary forest; (2) fitting a model using data from tropical and subtropical forest biomes only, appreciating that there are often regional differences in response to human impacts, both in terms of alpha (Phillips et al. 2017) and beta diversity (Newbold et al. 2016); (3) use of minimally-used primary vegetation as the baseline for compositional similarity models rather than primary vegetation; (4) more efficient use of data in the compositional similarity models, allowing us to account for additional habitat degradation related to roads and human population density (Rouget et al. 2006); and (5) attempting to incorporate into projections the impact of plantation forests, which can cause significant biodiversity loss particularly when expanding at the expense of primary forest (Koh & Wilcove, 2008; Gibson et al. 2011; Phillips et al. 2017). Incorporating the effect of plantation forests within secondary vegetation may cause underestimates of BII; in the absence of global layers of plantation forest, we will need to undertake a sensitivity analysis by excluding the impact of plantation forests (as in Newbold et al. 2016a) to provide an upper bound on the possible BII values. New land-use maps that are being produced with finer land-use classes (e.g., Hurtt et al. in prep) should also allow more accurate assessments of BII. In addition, parameter uncertainty in both the abundance and compositional similarity models could be incorporated to provide uncertainty bounds on estimates and trends. This will be important especially for urban areas, where the data used here are limited and so projected diversity will be more uncertain.

Limitations

We have attempted to provide a method for tracking annual change in biodiversity indicators in response to human impacts in the hope that these can help inform policy at national and international levels by highlighting key areas for conservation and monitoring progress towards conservation targets. However, there are a number of caveats that must be considered as well as limits to the interpretation of results. Firstly, pressure data vary in their resolution and in their accuracy. This is particularly important for road networks, which can grow rapidly; however the data are only available as a static layer, and the completeness varies regionally. Static road layers may still provide insights into biodiversity responses: for instance, roads built pre-2000 were associated with forest loss in the following decade in Borneo (Bicknell et al. 2015). However, other linear infrastructure, such as gas lines, can also have important consequences for biodiversity that are not included here (Laurance et al. 2009). In addition, human population density was interpolated between time steps and, as the data are downscaled using an areal-weighting approach, its resolution at the pixel level varies depending on the size of the input areal unit (Loyd et al. 2017). Such difficulties mean that while we have estimated BII at a 30" resolution, these data are most suitable for assessing average changes across larger pixels or areas (e.g. at a country level) and across broader time steps, rather than focussing on pixel-by-pixel and year-on-year changes. This is especially true as pressure variables include both spatial and temporal autocorrelation and the underlying diversity data does not allow for temporal dynamics of change (De Palma et al. 2018).

The implementation of BII used here may still underestimate biodiversity loss. One reason is that the compositional similarity metric implied by the original definition of BII (Scholes & biggs 2005) is quite permissive, in that the species abundance distribution could be completely reorganised without reducing BII, provided that the total abundance of originally-present species is not reduced and novel species are not introduced. Therefore, a region with high BII can still under some circumstances have shown strong losses in other aspects of diversity (see Faith et al. 2007 for more details). Using a combination of beta-diversity metrics may provide a more comprehensive assessment of the state of diversity (Socolar et al. 2016; Hillebrand et al. 2018) and is a natural avenue for future development of BII. In addition, using a baseline of minimally-used primary vegetation may lead to optimistic results (Purvis et al. 2018): in the PREDICTS database, minimally-used vegetation is the closest available proxy to the ideal 'pristine' baseline, but in many cases is simply the 'least disturbed' baseline (Kopf et al. 2015), as these sites may have suffered human impacts either directly or as spillover effects from impacts in the surrounding landscape. However, truly undisturbed sites are relatively rare – and becoming more so (Sloan et al. 2014; Venter et al. 2016).

Conclusion

Although estimating how BII has changed across space and time includes many underlying assumptions and uncertainty, the approach we have used goes beyond our previous implementation of BII by producing annual estimates based on time-varying data on pressures. These annual estimates provide a useful tool for policy makers hoping to track progress towards national and international targets, and for assessing the state of nature.

Declaration
The authors declare no competing financial interests.

Data availability
The data used here will be openly available for download from the NHM data portal (data.nhm.ac.uk) along with summary statistics for land use and BII for each country and region.

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Figures

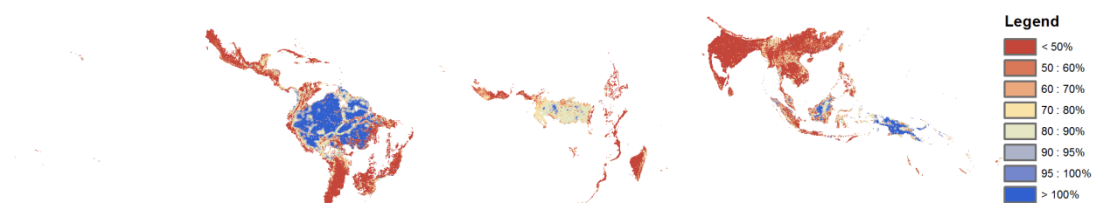Figure 1: Map of BII 2012 for tropical forested biomes at 30 arc second resolution.

Figure 2: Average change in BII over time at the country level, across different subregions. Change was calculated as the log-response ratio (LRR) of 2012 and 2001 values. A value of zero indicates no change (identified by the dashed line), negative values indicate a decline over time, and positive values indicate an increase in BII over time. Wider, lighter boxes include all countries; narrower, darker boxes use data for countries where BII has been calculated for at least 50% of their area.
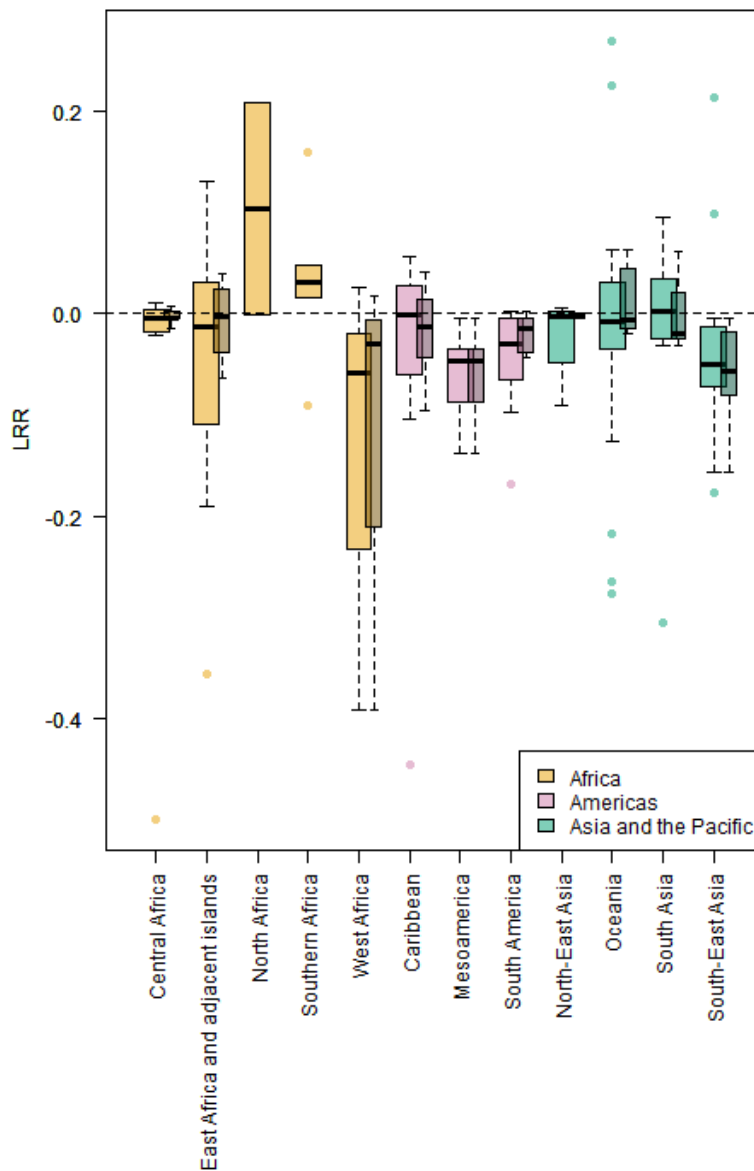
Figure 3: Change in BII over time plotted against the change in GDP per capita for each country. Change was calculated as the log-response ratio of 2012 and 2001 values. A value of zero indicates no change, negative values indicate a decline from 2001 to 2012, and positive values indicate an increase in BII between 2001 and 2012. Note that not all countries have available data on GDP per capita for the years 2001 and 2012 so some countries are excluded from this plot. Colours represent the different regions; colours are also shaded light to dark to represent low, middle and high starting values of GDP.