



Considering habitat conversion and fragmentation in characterisation factors for land-use impacts on vertebrate species richness



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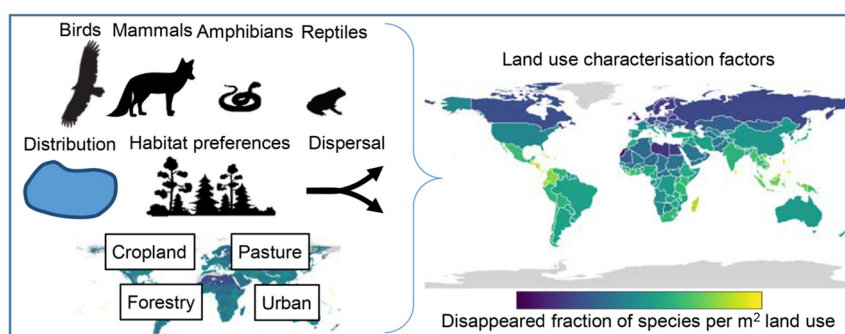
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HIGHLIGHTS

- Taxonomic and regionally specific assessments improve LCA accuracy.
- Considering fragmentation generally results in higher LCA characterisation factors.
- Characterisation factors indicate highest regional species loss in temperate regions.
- In terms of global extinctions, subtropical regions are most vulnerable to land use.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 21 May 2021

Received in revised form 9 August 2021

Accepted 13 August 2021

Available online 18 August 2021

Editor: Deyi Hou

Keywords:

Life cycle assessment (LCA)

Life cycle impact assessment (LCIA)

Land-use

Fragmentation

Species-area relationship (SAR)

Terrestrial biodiversity

ABSTRACT

Human land use is one of the primary threats to terrestrial species richness and is considered a priority for meeting global sustainability and biodiversity targets. Decision-support tools, such as life cycle assessment (LCA), are widely used for developing strategies to achieve such objectives. Currently available life cycle impact assessment (LCIA) methods apply the countryside species-area relationship (c-SAR) to quantify habitat conversion impacts on species richness. However, additional effects of habitat fragmentation are yet ignored in these assessments. We use the species-habitat relationship (SHR), an adaptation of the c-SAR that considers both habitat conversion and fragmentation effects, to develop a new set of land-use characterisation factors for 702 terrestrial ecoregions (in 238 countries), four land-use types (urban, cropland, pasture, and forestry), and four taxonomic groups (amphibians, birds, mammals, and reptiles; plus the aggregate of these vertebrate groups). The SHR generally predicts higher per-area impacts of land-use than the impacts estimated by the c-SAR (a median relative difference of +9%), indicating that land-use impacts may be systematically underestimated when ignoring fragmentation effects. Whereas per-area impacts of land-use on regional species richness are highest in temperate regions, reflecting the diminished extent of natural habitat, per-area impacts of land-use on global species richness are highest in the subtropics, reflecting the importance of tropical regions and islands to global vertebrate species diversity. The large variety in magnitude of land-use impacts across the world's regions emphasizes the importance of regionalised assessments. The set of characterisation factors proposed here can be readily used in environmental decision-making.

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1. Introduction

Habitat conversion is considered one of the key drivers for global declines in terrestrial species richness (IPBES, 2019). Agriculture, covering ~40% of the ice-free land (Ramankutty et al., 2008), is the dominant contributor, but also forestry and expansion of urban settlements instigate disappearance of natural habitat globally (Ellis and Ramankutty, 2008). As human land-use is projected to further expand (Kehoe et al., 2017), global targets and agreements for meeting human needs whilst preserving biodiversity have been established (Tittensor et al., 2014; UN, 2019).

Development of strategies to achieve sustainability targets depend on quantitative understandings of environmental impacts of human activities. Life cycle assessment (LCA) is a standardised method to quantitatively assess cradle-to-grave environmental impacts of products and processes (Hellweg and Mila i Canals, 2014). It is widely used to compare environmental consequences of products or technologies to capture potential trade-offs between different impacts and to identify impact hotspots (Finnveden et al., 2009).

Chaudhary et al. (2015) developed a life cycle impact assessment (LCIA) methodology for characterising land-use impacts per m² of various land-use types on vertebrate and plant species richness, based on the countryside species-area relationship (c-SAR) (Pereira and Daily, 2006), a species-area relationship (SAR) variant that considers habitat suitability. They used this method to assess land-use impacts of alternative bioethanol production technologies. The characterisation factors they developed are currently recommended by the life cycle initiative (Jolliet et al., 2018) and implemented in the LC-IMPACT methodology (Verones et al., 2020). Because of the direct applicability to land-use data, this method has been used in various global impact assessments, for example to address consumption-based land-use impacts along global value chains (Chaudhary and Brooks, 2019; Chaudhary and Kastner, 2016; Marques et al., 2019), to quantify impacts of different land-use intensities (Chaudhary and Brooks, 2018), or to use it in combination with other impacts for estimating human footprints (Verones et al., 2017b).

However, the c-SAR considers impacts of habitat conversion only, neglecting other land-use impacts that may also negatively affect biodiversity, such as habitat fragmentation (Kuipers et al., 2019b). The species-fragmented area relationship (SFAR) (Hanski et al., 2013) is a SAR variant that considers habitat fragmentation through the metapopulation capacity (Hanski and Ovaskainen, 2000). Larrey-Lassalle et al. (2018a, 2018b) combined the c-SAR with the SFAR to develop a set of characterisation factors (CFs) for land-use impacts on birds in ecoregions covering forest biodiversity hotspots ($n = 283$). However, the metapopulation capacity requires population-specific information for scaling the effect of fragmentation on immigration, emigration, and extinction rates (Hanski and Ovaskainen, 2000), restricting the applicability of this method across regions and taxa, as such data is not broadly available.

Another approach for considering both habitat conversion and fragmentation in SAR models is to incorporate the equivalent connected area (ECA) concept (Saura et al., 2011), as proposed first by Garcia-Ulloa et al. (2016). The ECA is a measure of effectively connected habitat considering species dispersal distances and permeability of the landscape (i.e., matrix) and can be parametrised relatively easily compared to the metapopulation capacity. Kuipers et al. (2021) developed the species-habitat relationship (SHR) by integrating the c-SAR and the ECA to consider both habitat suitability and connectivity in a SAR approach designed for global applications and showed that neglecting fragmentation effects may lead to, on average, 9% underestimation of land-use impacts on non-flying mammals globally.

Here, we present a new set of CFs for land-use (i.e., occupation) and land-use change (i.e., transformation) impacts on vertebrate species richness considering the combined effects of habitat conversion and fragmentation by adopting the SHR and applying it across vertebrate

taxa, ecoregions, and land-use types. The proposed CFs cover 702 terrestrial ecoregions, four land-use types (i.e., urban, cropland, pasture, and forestry), and four taxonomic groups (amphibians, birds, non-flying mammals, and reptiles), based on globally available land-use and species data. These CFs can be readily used in impact assessments, e.g., in LCA or environmentally extended input output analyses (EEIOA).

2. Material and methods

2.1. Impacts on species richness

2.1.1. Species-habitat relationship

SARs denote the relationship between species richness and area and can be used to estimate change in regional richness due to land-use. The SHR considers the effects of change in land type suitability and connectivity on species richness by replacing the area variable of the c-SAR by the ECA (Eq. (1)) (Kuipers et al., 2021).

$$PDF_{g,j,reg} = 1 - \left(\frac{H_{g,j}}{H_{g,j,ref}} \right)^{z_{g,j}} = 1 - \left(\frac{\sum_i h_{g,i,j} \cdot ECA_{g,i,j}}{\sum_i h_{g,i,j} \cdot ECA_{g,i,j,ref}} \right)^{z_{g,j}} \quad (1)$$

PDF is the potentially disappeared fraction of species in taxon g and region j , and is the recommended LCA metric for damage to ecosystems (Verones et al., 2017a). H is the suitable connected habitat and defined as the sum of the habitat suitability (h) to taxon g multiplied with the equivalent connected area (ECA) of all land types in region j (this includes both natural land cover and anthropogenic land-use types) (Eq. (2)).

$$H_{g,j} = \sum_i h_{g,i,j} \cdot ECA_{g,i,j} \quad (2)$$

h is the habitat suitability of land type i to taxon g in region j , and z is the SHR slope for taxon g and region j (Pereira and Daily, 2006). The ECA is the effectively connected area of land type i for taxon g in region j (Saura et al., 2011). The difference of the ECA in the current and in the reference (*ref*) state forms the basis for the change in PDF. The PDF can be converted to species loss ($S_{g,j,loss}$) by multiplying it with the original number of species in the region ($S_{g,j}$).

Land type suitability is defined as the proportion of species of taxon g occurring in land type i relative to the total number of species (S) of taxon g in region j , raised to the power $1/z$ (Eq. (4)) (Chaudhary and Brooks, 2018; Martins and Pereira, 2017; Pereira et al., 2014).

$$h_{g,i,j} = \left(\frac{S_{g,i,j}}{S_{g,j}} \right)^{1/z_{g,j}} \quad (3)$$

The ECA (expressed in unit of area) is the effectively connected area of land type i for species group g in region j , based on the number and size (a) of individual patches m and n of land type i and the probability of dispersal (p) between each pair of patches m and n (Eq. (4)) (Saura et al., 2011).

$$ECA_{g,i,j} = \left(\sum_{m,n} a_{i,j,m} \cdot a_{i,j,n} \cdot p_{g,i,j,mn} \right)^{0.5} \quad (4)$$

The probability of dispersal is dependent on the least-cost distance (w) between patches m and n and the median dispersal distance (α) of the species of taxon g in land type i and region j (Eq. (5)).

$$p_{g,i,j,mn} = e^{-w_{g,i,j,mn}/\alpha_{g,i,j}} \quad (5)$$

The least-cost distance (w) between patches m and n is the matrix-permeability-weighted length of the route that results in the shortest distance connecting the two patches (Garcia-Ulloa et al., 2016; Saura and Pascual-Hortal, 2007). The permeability-weighted length is defined as the distance (d) travelled through matrix type k multiplied with the

resistance (r) of the species of taxon g in land type i and region j to this matrix type (Eq. (6)).

$$w_{g,i,j,mn} = \sum_k d_{i,j,k,mn} \cdot r_{g,i,j,k} \quad (6)$$

The resistance of the species of taxon g in land type i and region j to matrix type k is dependent on the overlap of species between land type i and matrix type k (Eq. (7)).

$$r_{g,i,j,k} = 1 - \frac{S_{g,i,j,k}}{S_{g,i,j}} \quad (7)$$

If there is a full overlap between the species in land type i and matrix type k , the resistance equals 0, meaning that the matrix can be crossed without any cost, effectively forming a corridor for dispersal. Thus, relatively permeable matrix types form corridors and so-called “stepping stones”, increasing patch connectivity (Saura and Pascual-Hortal, 2007).

Compared to the c-SAR, which considers the total amount of habitat in a landscape, the SHR considers amount and connectivity of habitat (dependent on the species group) via matrix resistance and least-cost distances between habitat patches (based on the spatial landscape configuration), species dispersal distances, migration probability between habitat patches, and sizes of individual habitat patches (Fig. 1). By including these components in the calculation of land use CFs, effects of both change in habitat amount as well as fragmentation are considered.

2.1.2. Global extinction probability

Because of the overlap of species across regions, regional extinctions do not equate global (i.e., irreversible) extinctions. Only a proportion of species that become extinct regionally will be extinct globally, based on species endemism and extinction risk. The global extinction probability (GEP) addresses the potential contribution of regional species loss to global species extinctions, considering endemism and the threat status of the regional species pools (Kuipers et al., 2019a), and can be used directly to translate regional impacts to potential global impacts (Dorber et al., 2019) (Eq. (8)).

$$PDF_{g,j,glo} = PDF_{g,j,reg} \cdot GEP_{g,j} \quad (8)$$

2.2. Land occupation and transformation characterisation factors

Land-use CFs attribute regional impacts on species richness to the per-area effects of several land-use types. In LCA, land-use impacts are differentiated by land occupation (land-use) and land transformation (land-use change) impacts. Land occupation CFs indicate the PDF/m² of land-use type i . Land transformation CFs are time-integrated impact

factors (PDF·years/m² of land-use type i) considering the regeneration time after a land-use pressure is released (Curran et al., 2016; Milà i Canals et al., 2007). The CFs can be calculated for both regional extinctions by using the damage function of Eq. (1), or for global extinctions by using the damage function of Eq. (8).

Land-use CFs typically comprise three aspects: i) a regional impact indicator (calculated by the damage function in Eqs. (1) or (8)), ii) a conversion factor for per-area land use impacts, and iii) a distribution factor to attribute the impacts to the various land-use types. There are two approaches for converting the regional impacts to the regional per-area impacts of land-use: the average and marginal approach (Fig. S4.1) (Huijbregts et al., 2011). The marginal approach is recommended only for assessing marginal (i.e., small) changes to the environment, whereas the average approach is recommended for assessments at larger scales (Joliet et al., 2018).

2.2.1. Average characterisation factors

Using the average approach, occupation CFs are calculated by dividing the impact indicator by the total regional amount of land-use and multiplying this with the land-use distribution factor (Eq. (9) and Fig. S4.1) (Chaudhary et al., 2015; de Baan et al., 2013b).

$$CF_{g,i,j,occ,avg} = PDF_{g,j} \cdot A_{lu,j}^{-1} \cdot q_{g,i,j} \quad (9)$$

Here, PDF is the impact indicator for taxon g in region j , A is the total area of all land-use types combined (lu), and q is the distribution factor for attributing the impacts on taxon g in region j to land-use type i .

The distribution factor is dependent on the area (A) weighted by the suitability of land-use type i to the taxon g in region j , relative to the total suitability weighted area of the land-use types (Eq. (10)) (Chaudhary et al., 2015; de Baan et al., 2013b). Relatively high impacts are attributed to land-use types with a high proportion of the total land-use area and low suitabilities to the regional species pool.

$$q_{g,i,j} = \frac{(1 - h_{g,i,j}^{z_{g,i,j}}) \cdot A_{lu,j}}{\sum_{i|lu} A_{i|lu,j} \cdot (1 - h_{g,i|lu,j}^{z_{g,i,j}})} \quad (10)$$

Land transformation CFs are calculated by multiplying the occupation CFs with half the regeneration time (t) of taxon g in land-use type i and region j (Eq. (11)) (independent of the average or marginal approach) (Chaudhary et al., 2015; de Baan et al., 2013b).

$$CF_{g,i,j,tra} = CF_{g,i,j,occ} \cdot 0.5t_{g,i,j} \quad (11)$$

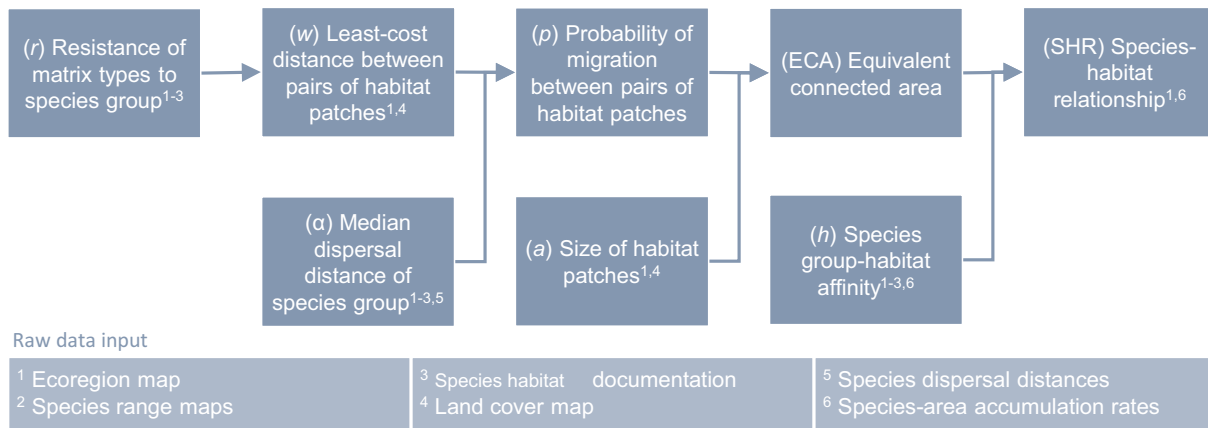


Fig. 1. Diagram of the species-habitat relationship (SHR) model parameters and data requirements.

2.2.2. Marginal characterisation factors

Instead of calculating the average per-area impacts of land-use, the marginal approach considers the effects of marginal change in land-use (Fig. S4.1). This is achieved by taking the partial derivative of the damage function (Eq. (1)) by the change in suitable connected habitat (Eq. (12)) (Chaudhary et al., 2015; de Baan et al., 2013b). Change in suitable connected habitat can be defined as the difference between current suitable connected habitat and the suitable connected habitat in the reference state as $\Delta H_{g,j} = H_{g,j} - H_{g,j,ref}$.

$$\frac{\partial PDF_{g,j}}{\partial \Delta H_{g,j}} = H_{g,j,ref}^{-1} \cdot z_{g,j} \cdot \left(\frac{H_{g,j}}{H_{g,j,ref}} \right)^{z_{g,j}-1} \quad (12)$$

To convert the marginal impacts of land-use type i to the impacts per m^2 , the marginal damage function (Eq. (12)) is multiplied with the conversion factor converting change in suitable connected habitat. To attribute the impacts across the land-use types the per-area impacts are multiplied with the land-use distribution factor (q ; Eq. (13)), identical to the distribution factor used in the average approach (Eq. (10)).

$$CF_{g,i,j,occ,mar} = \frac{\partial PDF_{g,j}}{\partial \Delta H_{g,j}} \cdot \frac{\Delta H_{g,j}}{A_{i,j}} \cdot q_{g,i,j} \quad (13)$$

Marginal transformation CFs are calculated by multiplying the marginal occupation CFs with half the regeneration time (t) of taxon g in land-use type i and region j (Eq. (11)).

2.2.3. Aggregated characterisation factors

Regionally and land-use-specific taxon-aggregated (\bar{g}) CFs are calculated as the average over the regional land-use CFs across the taxa (Eq. (14)) (Verones et al., 2015). This means that each taxon receives equal weight, independent of the number of species within each taxon present in the region.

$$CF_{\bar{g},i,j} = \sum_g^N CF_{g,i,j} \cdot N_j^{-1} \quad (14)$$

Here, CF is the taxon, land-use type, and regionally specific characterisation factor and N is the number of taxa present in the region.

To ease application in country-based impact assessments, the ecoregion-level characterisation factors are also aggregated to the country level as the average CFs weighted by the ecoregion (j) area (A) shares per country (u) (Eq. (15)).

$$CF_{g,i,u} = \sum_j CF_{g,i,j} \cdot \frac{A_{j,u}}{A_u} \quad (15)$$

2.3. Model parametrisation

Local impacts (affinities at 5' grid scale) are upscaled to ecoregional impacts via the SHR. Characterisation factors are calculated at the ecoregion-level. Terrestrial ecoregions are biogeographical units that are relatively homogeneous in their vegetation and species pool (Olson et al., 2001). The proposed CFs cover 702 of the 825 terrestrial ecoregions based on available land-use and species data as CFs cannot be calculated for ecoregions absent of land-use or species data points. We derived taxon-, region-, and scale-dependent slopes (i.e., z values) for the SHR from Storch et al. (2012) (Table S1.2).

Land-use and land cover data in each ecoregion was based on the GLOBIO 2015 land use map (Schipper et al., 2020). To reduce computation times and in line with other global land-use impact assessments (Chaudhary et al., 2015, 2016; Marques et al., 2019; Verones et al., 2017b), the GLOBIO 2015 map was resampled from a resolution of 10" (300 m) to 5' (9 km) based on the modal values. Furthermore, the

GLOBIO 2015 land cover and land-use types were aggregated to eight major land types. Four of these are natural land cover types (forests, grasslands, deserts, and rock and ice) and four of these are anthropogenic land-use types (urban, cropland, pasture, and forestry). The GLOBIO "light pasture" landcover class was replaced by the original European Space Agency Climate Change Initiative land cover (ESA, 2017) as this class indicates natural habitat that is used mainly for extensive grazing (Alkemade et al., 2013) and is not appropriate for aggregation with more intensive pastoral practices. The area and ECA of these land types per ecoregion can be found in the Supporting Information (Tables S1.4 and S1.5, respectively).

The reference land cover map, used for the ECA in the reference state, indicates the land cover absent of human land-use. This reference state land cover map is based on the current GLOBIO 2015 land-use map with all land-use cells replaced by original natural land cover as defined by the ISLCS II Potential Natural Vegetation Cover map (Gallego-Zamorano et al., 2020; Ramankutty et al., 2010).

The taxon- and regional-specific land type suitability and matrix permeability values were derived from the regional number of species occurring in the land and matrix types. These regional land and matrix type-specific species numbers were obtained from species range maps and habitat occurrences documented by the International Union for Conservation of Nature (IUCN) covering 6490 amphibian species, 11120 bird species, 4179 non-flying mammal species, and 4923 reptile species (IUCN, 2020) (Tables S1.1 and S1.3).

The median dispersal distance of the taxon-, land type, and regional-specific species group (i.e., species of taxon g in region j that occur in land type i) was defined as the median of the natal dispersal distances of all individual species within this group. Bird and non-flying mammal dispersal distances were estimated from reported relationships between body mass (b), home range, and natal dispersal distance (Table 1) (Bowman, 2003; Bowman et al., 2002; Hilbers et al., 2016). Bats (*Chiroptera*) were excluded from the mammal analysis because of the uncertainty regarding the dispersal behaviour of this mammal order compared to other mammals. Bird and mammal body masses were extracted from the EltonTraits 1.0 database covering 9994 birds and 3696 (non-flying) mammals. The estimated median dispersal distances of the bird and mammal species groups per region and land type can be found in the Supplementary Information (Table S1.6 and Fig. S4.2).

There are no general allometric relationships available for the dispersal of reptiles and amphibians. Due to this data limitation and considering the land cover cell resolution of 9 km and the reported small dispersal distances for amphibians and (terrestrial) reptiles (Cushman, 2006; Smith and Green, 2005; Southwood and Avens, 2010; Trochet et al., 2014) we adopted the conservative assumption that amphibians and reptiles are unable to disperse over a distance of more than 9 km through unsuitable landcover, making them more susceptible to habitat fragmentation effects.

The GEP per taxon and ecoregion was extracted from Kuipers et al. (2019a) (Table S1.7) and can be applied directly to the regional impacts in this study to translate regional extinctions into potential global extinctions.

The taxon-, land-use type-, and regional-specific regeneration times for calculating the land transformation CFs were extracted from Chaudhary et al. (2015) (Table S1.8) (Curran et al., 2014).

Table 1

Relationships between bird and mammal body mass (b , in grams) and natal dispersal distance (D , in meters).

Taxon	Carnivorous	Non-carnivorous
Birds	$D = 12 \sqrt{2.1 \cdot 10^5 b^{1.13}}$	$D = 12 \sqrt{3.7 \cdot 10^4 b}$
Mammals	$D = 40 \sqrt{3.8 \cdot 10^2 b^{1.13}}$	$D = 40 \sqrt{5.4 \cdot 10^1 b}$

3. Results

The main result is the set of CFs for land occupation and transformation impacts on regional and global vertebrate species richness. We present taxon-specific (i.e., amphibians, reptiles, birds, and non-flying mammals) and taxon-aggregated characterisation factors using an average and marginal approach on the ecoregion (Tables S2.1–2.8) and country level (Tables S3.1–3.8). We were able to calculate taxon-aggregated characterisation factors for global impacts of at least one of the land-use types (i.e., urban, cropland, pasture, and forestry) for 702 of the in total 825 terrestrial ecoregions based on available land-use and species data. Correspondingly, we were able to calculate country-level impacts for 238 of the 257 countries listed by Eurostat. Here, we present the results of the average CFs at the ecoregion-level. Furthermore, here we focus on taxon-aggregated CFs rather than taxon-specific CFs. Average and marginal CFs, as well as taxon-specific and taxon-generic CFs for ecoregions and countries, can be found in the Supplementary Information (Tables S2.1–2.8 and S3.1–3.8).

CFs indicating regional and global land-use impacts varied on average by four orders of magnitude across the land-use types and regions (Fig. 2). Global CFs were generally three orders of magnitude smaller than regional CFs, suggesting that on average every 1000 regional species disappearances result in one global species extinction. Land occupation and transformation CFs have similar distributions (Fig. 3).

CFs indicating regional land-use are highest in the northern hemisphere (Fig. 3a–b), reflecting the relationship between the extent of human land-use (Fig. S4.1) and the resulting effects of habitat conversion and fragmentation on regional vertebrate species richness. The spatial distribution of land transformation effects largely reflects the distribution of the land occupation effects, although the generally larger regeneration times in the northern hemisphere emphasize high impacts in the regions north of the equator.

CFs indicating use impacts on global species richness are generally highest in the subtropics (Fig. 3c–d), reflecting species-rich regions

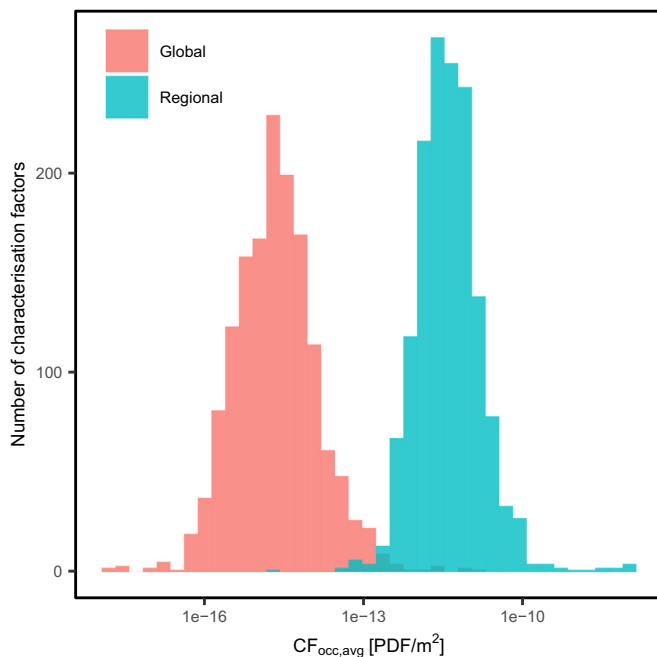


Fig. 2. Distribution of taxon-aggregated land occupation characterisation factors (per region and land-use type) for global and regional impacts (characterisation factors are distributed over a logarithmic scale). The darker colour indicates overlap between the distribution of the global and regional characterisation factors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Table S1.1) and vulnerabilities of species-communities characterised by the presence of endemic species (e.g., on tropical islands). Consequently, per-area impacts of land-use on global species richness are projected to be highest in ecoregions located in Oceanic, Indomalayan, Neotropic, and Australasian realms (Fig. 4).

The country-aggregated characterisation factors reflect the spatial pattern of the ecoregions (Fig. 5), highlighting per-area impacts of land-use in tropical and insular countries (e.g., Sri Lanka and the Philippines) whereas lower per-area impacts of land-use are expected at higher latitudes (e.g., Canada and Scandinavia), or in arid countries (e.g., Egypt and Libya).

The magnitude of the impacts of the different land-use types largely depends on the suitability of the land-use types to the regional species community. There is a large variation in species community responses to these land-use types between the regions (Fig. S4.5), revealing no obvious general distinction between the per-area impacts of each land-use type (Fig. 6).

CFs calculated by the marginal approach are systematically higher than those calculated by the average approach (as illustrated by Fig. S4.1). However, the difference between the two methods is generally small and only becomes substantial if a large proportion of the natural land has been modified by human land-use.

Comparing the CFs calculated by the SHR with CFs calculated with the traditional c-SAR (not considering fragmentation effects) on a regional basis reveals that the SHR generally predicts higher per-area impacts of land-use than the c-SAR (a median relative difference of +9%). On the aggregate level, the CFs calculated by the SHR have a similar distribution as the CFs calculate by the c-SAR, but the set of CFs calculated with the SHR contains more large CFs than the c-SAR. This is reflected by the shift to the right of SHR CFs in Fig. 7. Per region, the SHR does not systematically calculate higher impacts than the c-SAR because the SHR also considers fragmentation of the natural land types in the reference state, meaning that the c-SAR and SHR have different reference states.

There is no biogeographical bias in SHR CFs predicting higher impacts as habitat change is the dominant factor explaining differences between c-SAR and SHR CFs. SHR predicts higher impacts if i) fragmentation effects contribute to the total land use impacts and ii) the landscape has become increasingly fragmented. The c-SAR predicts higher impacts if habitat connectivity remained unchanged or increased. Comparing c-SAR- and SHR-based cropland occupation CFs for impacts on global species richness shows that in most ecoregions the SHR predicts higher impacts ($n = 454$, c-SAR predicts higher impacts in 193 ecoregions; Fig. 8). This implies that most ecoregions have become increasingly fragmented.

4. Discussion

CFs were calculated for ecoregions (and countries) where land-use data was available at a resolution of 5' (9 km). To assess potential land-use impacts in regions for which no CFs could be developed we suggest using CFs of neighbouring and comparable regions. Furthermore, CFs could only be calculated for regions with species data points present. Regional species data was obtained from the IUCN range maps, IUCN habitat occurrence documentation (IUCN, 2020) and generic species body mass data (Wilman et al., 2014). For this reason, only terrestrial vertebrate species were assessed as the distribution and habitat occurrences of other terrestrial species (e.g., plants or insects) are not globally available. To calculate CFs for amphibians and reptiles we assumed, despite the uncertainty and global unavailability regarding their dispersal distances, and based on the little available data (Cushman, 2006; Smith and Green, 2005; Southwood and Avens, 2010; Trochet et al., 2014), that they would not disperse over distances of 9 km or more. This means that the CFs potentially overestimate fragmentation effects on amphibians and reptiles.

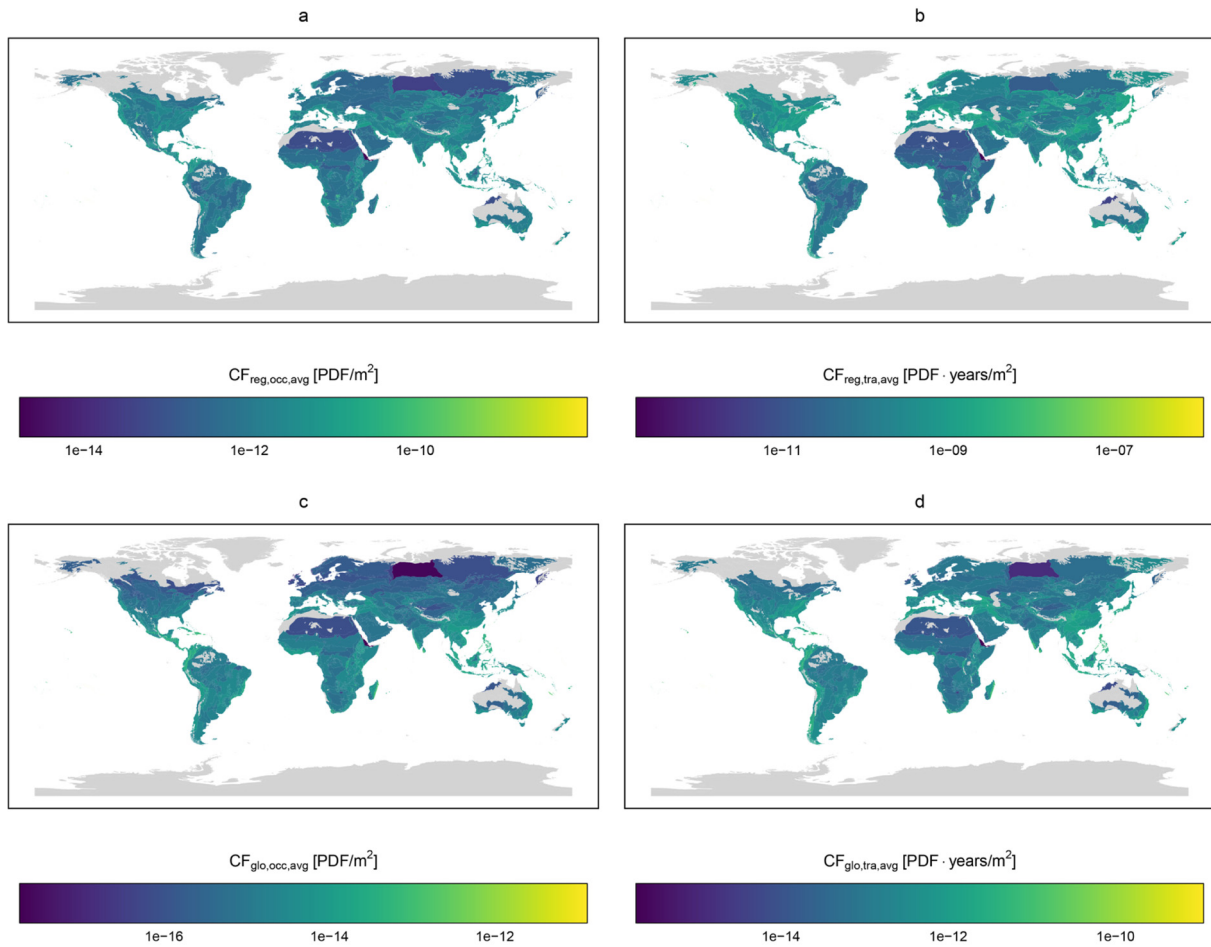


Fig. 3. Taxon aggregated (average) characterisation factors for croplands as an example. a) occupation impacts on regional species richness, b) transformation impacts on regional species richness, c) occupation impacts on global species richness, and d) transformation impacts on global species richness (logarithmic scales). Gray signifies no data, this can indicate absence of cropland in these regions, or missing species data. These figures for urban, pasture, and forestry land-use can be found in the Supplementary Information (S4.2–4.4).

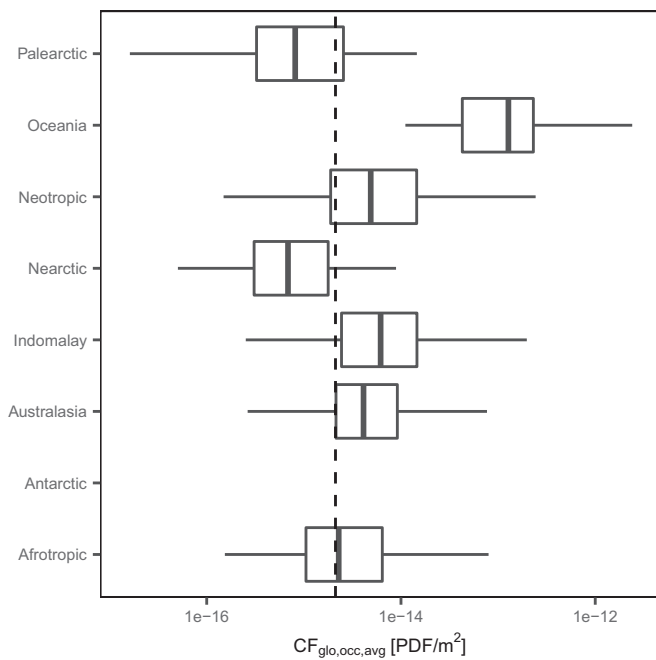


Fig. 4. Taxon-aggregated (average) characterisation factors (CFs) for land occupation impacts (across the land-use types) on global species richness (logarithmic scale). The dashed line indicates the global mean.

The CFs varied several orders of magnitude across the ecoregions and land types indicating that the per-area impacts of land-use can be very different from region to region, emphasizing the importance of regionalised land-use impact assessments (Chaudhary et al., 2016). Furthermore, although the responses to the various land-use types were different within the regions, the responses to the land-use types differed across the regions, further stressing that regionalised impact

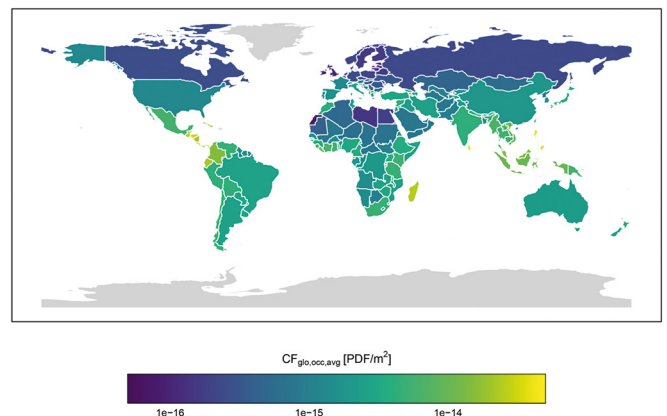


Fig. 5. Cropland (average) occupation characterisation factors for impacts on global species richness on the country-level.

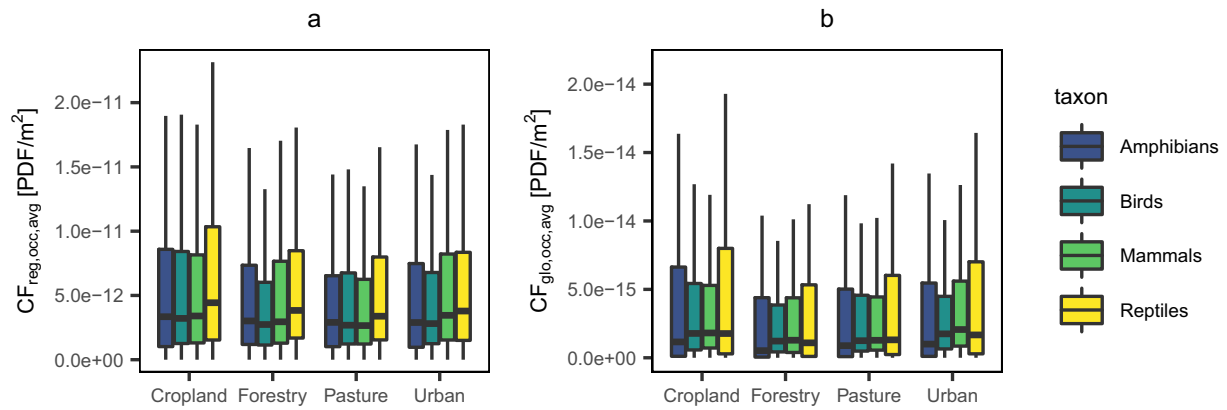


Fig. 6. Taxon-specific (average) land occupation characterisation factors (CFs) for the land-use types. a) characterisation factors for regional impacts and b) characterisation factors for global impacts (note the difference in scale between the regional and global characterisation factors). The dashed line indicates the mean across the taxa and land-use types.

assessments are important to adequately characterise land-use impacts at the global scale.

Per-area impacts of land-use were highest in the northern hemisphere where much of the natural habitat has been converted into human land-use types. The SAR predicts progressively increasing per-area impacts of land-use change if the proportion of remaining natural habitat diminishes (illustrated by the pressure-response curve in Fig. S1) (Pereira and Daily, 2006). The relative magnitude of land-use impacts on global species richness, however, shifts toward regions at lower latitudes characterised by high species richness and higher presence of endemic species. Per-area impacts of land-use on global species richness are especially high in tropical islands. Hence, in these regions, sustainable land-use management will be of the utmost importance to balance land-use practice with biodiversity preservation.

The difference between CFs calculated by the average and marginal approach become increasingly apparent as the proportion of remaining natural habitat decreases with higher per-area impacts calculated by the marginal approach compared to the average approach. Whereas CFs calculated by the average approach reflect the cumulative per-area impacts of land-use practices up to the current situation, CFs calculated by the marginal approach reflect potential additional per-area

impacts of land-use compared to the current state (Huijbregts et al., 2011). The choice between a marginal or average approach depends on the intended purpose of the LCA (Huijbregts et al., 2011). When comparing LCA impacts, it is important that impacts based on average CFs are compared to other impacts calculated with average CFs only and that impacts based on the marginal approach are compared to other impact based on the use of marginal CFs.

The SHR is a SAR variant that replaces the area variable (A) in the c-SAR with the ECA. Whereas the area (A) in the c-SAR reflects the total amount of area of a specific land type, the ECA reflects the effectively connected area considering the spatial configuration of the landscape and the matrix permeability for and the median dispersal distance of the species group occurring in the land type. The ECA is per definition equal to or smaller than the total area of a certain land type. Consequently, the SHR considers change in both area and connectivity of the landscape. This leads to different results compared to the c-SAR as apart from the total area, the connectivity of land types also changes. Because we also considered natural fragmentation of the natural mosaic of land cover types (i.e., forests, grasslands, deserts, and rock and ice), the reference states are different in the c-SAR and SHR. This implies that the SHR does not systematically predict higher impacts than the c-SAR, although it most often does as fragmentation is generally more extreme

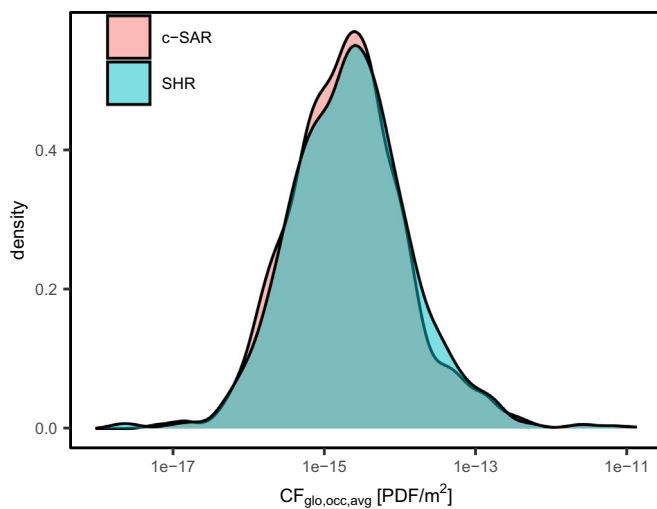


Fig. 7. Density plots of the distribution of taxon-aggregated (average) land occupation characterisation factors (CFs) for impacts on global species richness calculated using the countryside SAR (c-SAR) and species-habitat relationship (SHR) (logarithmic scale on the x-axis). Across the ecoregions, characterisation factors calculated by the SHR are a median of 9% higher than the characterisation factors calculated by the c-SAR.

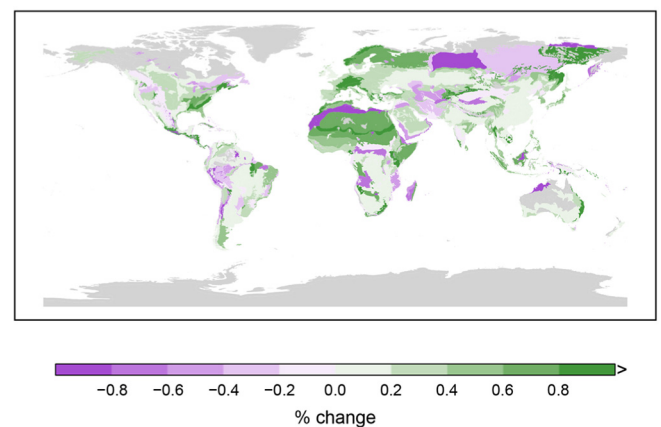


Fig. 8. Percentage change between taxon-aggregated (average) cropland occupation characterisation factors (CFs) for impacts on global species richness calculated using the species-habitat relationship (SHR) relative to the countryside SAR (c-SAR). Negative values (purple) indicate SHR CFs that are lower compared to c-SAR CFs and positive values (green) indicate SHR CFs that are higher compared to c-SAR CFs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in partially human-modified landscapes compared to completely natural landscapes.

Many global land-use assessments (Chaudhary and Brooks, 2018, 2019; Chaudhary and Kastner, 2016; Marques et al., 2019; Verones et al., 2017b) based their approach on the c-SAR approach proposed by Chaudhary et al. (2015). We followed the same logic for calculating CFs as Chaudhary et al. (2015), but apart from using the SHR instead of the c-SAR there are also differences in the parametrisation of the model's variables, as explained below.

First, Chaudhary et al. (2015) based the habitat suitabilities (h) on local species data collected by de Baan et al. (de Baan et al., 2013a). Later, Chaudhary and Brooks (2018), used local data from the PREDICTS database (Hudson et al., 2017) to estimate habitat suitabilities to different land-use types and intensities. Because this data is not available across all taxonomic groups, regions, and land-use types, we used species-specific habitat occurrences documented by the IUCN (IUCN, 2020) (Tables S1.1 and S1.3). This approach is consistent across the taxonomic groups and regions, but it does not consider locally specific responses to land-use types.

Second, we differentiated various broad natural land cover types (i.e., forests, grasslands, deserts, and rock and ice) and calculated the habitat suitability of these types to the regional species community (Tables S1.4 and S1.5). Chaudhary et al. (2015), did not differentiate between natural land cover types and treated all natural land cover as one type with a habitat suitability of 1 (i.e., 100% of the regional species community occurs homogeneously across the natural land cover). By differentiating between natural land cover types, it matters whether suitable natural land cover or relatively unsuitable land cover is converted into human land-use types whereas this is not considered when the natural land cover types are undifferentiated. This means that the spatial configuration of the reference state is relevant in the approach proposed here because the original land cover types have different habitat suitabilities. If the habitat suitability would be 1 for all natural land cover types, the suitability-weighted area in the reference state would equal the size of the region.

Third, Chaudhary et al. (2015) used three SAR slopes (z values for forest, non-forest, and island ecoregions) for the ecoregions based on a meta-analysis from Drakare et al. (2006). Nevertheless, besides being dependent on evolutionary histories, SAR slopes are dependent on the scale of analysis with generally steeper slopes for larger regions (Martins and Pereira, 2017; Pereira and Daily, 2006; Storch et al., 2012). As ecoregion sizes differ substantially, we instead adopted taxon-, continent-, and scale-dependent SAR slopes from Storch et al. (2012) (Table S1.2).

Fourth, instead of combining the GlobCover (Bontemps et al., 2011) and Anthromes (Ellis et al., 2010) land classification maps, we used the GLOBIO4 land classification map for consistency.

Fifth, instead of using so-called vulnerability scores (Verones et al., 2015) to translate impacts on regional species richness into impacts on global species extinctions we used the GEP (Kuipers et al., 2019a), which is suitable for the direct application to relative species richness impact indicators such as the PDF.

Finally, because the SHR replaces area in the c-SAR with ECA, the first derivative of the SHR curve is calculated for the change in ECA weighted by habitat suitability for the calculation of CFs using the marginal approach. To calculate the marginal CFs per-area land-use, the marginal impacts by change in ECA need to be converted to the marginal impacts by change in area. Here, this is addressed by considering the effect of change in land-use area on the change in ECA (Eq. (13)).

5. Conclusion

Land-use affects biodiversity by converting and fragmenting natural habitat, reducing the viability of the natural species community (Bartlett et al., 2016; Crooks et al., 2017; Haddad et al., 2015; Newbold et al., 2015). Impact assessments provide valuable insight into these

pressure-response relationships and standardised decision-support tools, like LCA, inform where high impacts can be expected and which processes and pressures contribute to these impacts (Hellweg and Mila i Canals, 2014). For example, LCA may support decision-making in land-use planning and management by doing scenario assessments for production alternatives.

We propose a new set of characterisation factors that can be readily used in impact assessments like LCIA or EEIOA (Marques et al., 2019) to more accurately assess land-use impacts on biodiversity by considering the combined effects of habitat conversion and fragmentation. These land-use characterisation factors allocate higher vulnerabilities to fragmented regions, or to regions hosting a species community vulnerable to habitat fragmentation. Consequently, when used for the development of conservation strategies, regions that are vulnerable because of the combined effects of habitat conversion and fragmentation will be highlighted.

As more data on species dispersal distances, especially for amphibians, reptiles and flying mammals, becomes globally available, the model's parametrisation can be refined. Similarly, as comprehensive and spatially explicit data on regional and habitat-specific species occurrences becomes available for taxa other than the four vertebrate groups addressed here, the set of characterisation factors can be expanded to cover a broader range of species. Until then, the taxon-aggregated characterisation factors can function as a proxy for land-use impacts.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.149737>.

CRediT authorship contribution statement

Koen J.J. Kuipers: Conceptualization, Methodology, Software, Formal analysis, Writing – original draft, Writing – review & editing. **Roel May:** Conceptualization, Methodology, Writing – review & editing. **Francesca Verones:** Conceptualization, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Funding information

The contribution of KJKK was funded by NTNU Sustainability.

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