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Terrestrial Vertebrate Biodiversity Loss under Future Global Land Use Change Scenarios

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Abstract: Efficient forward-looking mitigation measures are needed to halt the global biodiversity decline. These require spatially explicit scenarios of expected changes in multiple indicators of biodiversity under future socio-economic and environmental conditions. Here, we link six future (2050 and 2100) global gridded maps (0.25° × 0.25° resolution) available from the land use harmonization (LUH) database, representing alternative concentration pathways (RCP) and shared socio-economic pathways (SSPs), with the countryside species–area relationship model to project the future land use change driven rates of species extinctions and phylogenetic diversity loss (in million years) for mammals, birds, and amphibians in each of the 804 terrestrial ecoregions and 176 countries and compare them with the current (1900–2015) and past (850–1900) rates of biodiversity loss. Future land-use changes are projected to commit an additional 209–818 endemic species and 1190–4402 million years of evolutionary history to extinction by 2100 depending upon the scenario. These estimates are driven by land use change only and would likely be higher once the direct effects of climate change on species are included. Among the three taxa, highest diversity loss is projected for amphibians. We found that the most aggressive climate mitigation scenario (RCP2.6 SSP-1), representing a world shifting towards a radically more sustainable path, including increasing crop yields, reduced meat production, and reduced tropical deforestation coupled with high trade, projects the lowest land use change driven global biodiversity loss. The results show that hotspots of future biodiversity loss differ depending upon the scenario, taxon, and metric considered. Future extinctions could potentially be reduced if habitat preservation is incorporated into national development plans, especially for biodiverse, low-income countries such as Indonesia, Madagascar, Tanzania, Philippines, and The Democratic Republic of Congo that are otherwise projected to suffer a high number of land use change driven extinctions under all scenarios.

Keywords: biodiversity; evolutionary history; future pathways; habitat loss; land use; species extinctions

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1. Introduction

The rapid decline in global biodiversity likely has major consequences for ecosystem functioning and human wellbeing [1], and therefore international agreements such as the United Nations sustainable development goals (SDGs; [2]) and the Convention on Biological Diversity Aichi targets [3] commit to reducing these losses. The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) has identified that reporting past, present, and future trends of biodiversity at global and regional levels and development of scenarios is key to help decision makers evaluate different policy options [4,5].

Importantly, habitat destruction and degradation due to human land use for commodity production is, and is expected to remain, the major driver of biodiversity loss [6]. It is therefore surprising that a recent literature review [7] concluded that biodiversity scenarios over the past 25 years have focused on the future direct impacts of climate change, with only a few exploring the biodiversity outcomes due to future land use change. Moreover, most biodiversity scenarios have focused on changes in species richness as the only indicator of biodiversity change [8,9]. To meet the call of the IPBES, and to project a more accurate picture of the future of biodiversity, we need advancements in both land use projections and in models that translate these projections onto changes in different aspects of biodiversity (e.g., taxonomic, genetic, functional). We present attempts to do both here.

Land-use harmonization products (LUH-1; [10]) delivered with the IPCC Fifth Assessment Report opened up new opportunities for exploring the impacts of a range of possible land-use trajectories on biodiversity. These products connect future scenarios calculated by multiple integrated assessment models (IAMs; [11]) with historical land use data into a single consistent, spatially gridded set of land-use change scenarios. They provide annual fractions of five land uses (primary vegetation, secondary vegetation, pasture, cropland, and urban) at the $0.5° \times 0.5°$ scale between 1500 and 2100 for four representative concentration pathway (RCP) scenarios [12]. Each RCP describes an alternative future climate scenario with a specific radiative forcing (global warming) target (e.g., 2.6, 3.4, 4.5, 6.0, or 8.5 W/m^2) to be reached by the end of the century through the adoption of mitigation efforts [9,11]. Radiative forcing under each scenario is often considered as a proxy for the expected amount of atmospheric warming [13].

However, the main limitations of above LUH-1 land-use datasets is their relatively coarse spatial resolution (0.5 degree) and a limited number of land use categories (five) per grid cell. Such a simplified representation of land use is due primarily to the computational complexity of the models underlying these datasets [7]. For accurately predicting impacts on biodiversity, both the location and intensity of future land-use change projections are important because certain regions host a disproportionately high number of endemic species [14] and because the responses of species can differ widely depending upon management intensity [15].

Recently, a new set of future scenarios has been developed using the so-called scenario matrix architecture approach [16]. These scenarios are based on the combination of RCPs (describing carbon emissions trajectories, [12]), and shared socioeconomic pathways (SSPs), that describe development and socio-economic trajectories [17,18]. Five SSPs have been developed (SSP-1 to SSP-5) providing different trajectories of future socio-economic development and including possible trends in population, income, agriculture production, food and feed demand, and global trade, as well as land use [19]. Within each SSP, climate policies such as afforestation can be introduced in order to reach a particular radiative forcing level target consistent with an RCP [20].

In 2017, as a part of the Coupled Model Intercomparison Project (CMIP6), the updated land use harmonization dataset (LUH2 v2f, [21]) for the period 2015–2100 was released (http://luh.umd.edu/data.shtml), providing annual gridded fractions of 12 land-use types at $0.25° \times 0.25°$ resolution under six scenarios varying in climate target (RCP) and shared socioeconomic pathways (SSPs). The dataset also provides annual land use maps for the past (850–2014). This is a major improvement over the previous coarse scale and simplified LUH1 dataset [11] and can enable the evaluation of past extinction rates, as well as the future biodiversity trajectories, under different RCP-SSP scenario combinations more accurately.

With regard to biodiversity models translating the land use change into biodiversity loss, previous studies [8,9] have employed the classic form of species–area relationship model (SAR) that assumes that no species can survive in any human land use, thereby potentially overestimating species loss. Chaudhary and Brooks [22] showed that the countryside SAR model [23,24], which accounts for the fact that some species are tolerant to human land uses, better predicts habitat loss driven extinctions on a global scale than do classic SAR. Chaudhary and Brooks [22] proposed and tested a novel approach to parameterize the countryside SAR by leveraging the species-specific habitat classification scheme database [25] and projecting the species extinctions (for mammals, birds, and amphibians) due to land use change to date in 804 terrestrial ecoregions [26]. Another advantage of the countryside SAR model is that it allows for allocating the total extinctions to individual land uses in the regions, and thereby enables the identification of major drivers of species loss [22,27,28].

It has been argued that in addition to species richness, phylogenetic diversity (PD; also referred to as evolutionary history) may be a useful indicator of the biodiversity value of a region (see, for example, [29–31]) because PD represents the evolutionary information within the set of species, and a higher PD may offer a region with more functional diversity via complementarity, resilience, and more options to respond to global changes [30,32–34].

Unlike species richness [8,9], no study to date has evaluated the loss of phylogenetic diversity under future global scenarios. This is primarily because the complete dated species-level phylogenies for large taxonomic groups [31,35,36], and straightforward methods that can translate species extinctions in a region into the loss of PD from the evolutionary tree in which these species are found, have only recently become available [37,38]. This is relevant because previous studies have shown that regions with high projected species extinctions might not overlap with regions projected with high PD loss [37].

Here, we project potential future extinctions and concomitant phylogenetic diversity (PD) loss for mammals, birds, and amphibians in each of the 804 terrestrial ecoregions (and 176 encompassing countries) associated with land-use changes to 2050 and 2100 under six alternative scenarios, and compare them to projected extinctions under current (2015) and past (850, 1900) land use extent. For comparison purposes, we also calculate the rate at which species are being committed to extinction in the past (850–1900), present (1900–2015), and future time slices (2015–2050 and 2015–2100) by dividing additional projected extinctions with the time interval (e.g., 85 years for 2015–2100) and the total species richness of the taxon (see methods, Equations (2) and (5)).

We feed the future gridded maps generated by the six RCP-SSP combination scenarios (RCP 2.6 SSP-1, RCP 4.5 SSP-2, RCP 7.0 SSP-3, RCP 3.4 SSP-4, RCP 6.0 SSP-4, and RCP 8.5 SSP-5) available from recent LUH2 dataset into the newly parameterized countryside SAR model (Chaudhary and Brooks [22]) to project the number of endemic species committed to extinction in each ecoregion as a result of future land use change. To project the associated evolutionary history of the three taxa committed to extinction in each ecoregion and country (in million years), we apply the novel approach recently proposed by Chaudhary et al. [37] that combines countryside SAR, species-specific evolutionary distinctiveness (ED) scores [31,39], and a linear relationship between the cumulative ED loss and PD loss derived through pruning simulations on global evolutionary trees [37]. We identify hotspot ecoregions and countries projected to suffer high biodiversity loss under each future scenario and also allocate the total extinctions and PD loss to individual human land use types to identify the major drivers in each ecoregion and country.

We found that the most aggressive climate change mitigation scenario coupled with a sustainable socio-economic trajectory (RCP2.6 SSP-1) results in the least land use change, and therefore projects the lowest global biodiversity loss in future. The potential biodiversity loss due to direct effects of climate change, although not modeled in this study, is also expected to be lowest under this scenario with least warming. This demonstrates that global climate and biodiversity goals can be aligned, but this entails strong land use change regulations, reduced human consumption, high global trade, and technological innovations as foreseen in this scenario. Land use change under other five scenarios is projected to cause 2–4 times higher species extinctions and phylogenetic diversity loss than under sustainable RCP2.6 SSP-1 scenario, due to accelerated clearing of natural vegetation in species rich, low-income tropical countries of Africa, Latin America, south-east Asia, and the pacific. Comparison of impacts under two scenarios with the same socio-economic pathway (SSP-4), but different climate targets (RCP3.4 and RCP6.0), revealed that climate mitigation strategies that require natural land clearing to make way for biofuel crops in the tropical countries can lead to high biodiversity loss, thereby presenting a trade-off with climate goals. These results highlight that strategies to mitigate climate change need to be accompanied by sustainable socio-economic pathways, as well as habitat preservation in order to ensure a win-win situation for global climate and biodiversity goals.

2. Materials and Methods

2.1. Future Scenarios

Future land use maps at an annual interval (2015–2100) derived using six combinations of shared socio-economic pathways (SSPs) and representative concentration pathways (RCP) are currently available at land use harmonization project (LUH2v2f, [21]) website (http://luh.umd.edu/data.shtml): The are RCP 2.6 SSP-1, RCP4.5 SSP-2, RCP 7.0 SSP-3, RCP 3.4 SSP-4, RCP 6.0 SSP-4, and RCP 8.5 SSP-5.

The SSP-1 RCP 2.6 scenario [40] was simulated using the integrated model to assess the global environment (IMAGE) [41]. The RCP 3.4 SSP-4 and RCP 6.0 SSP-4 scenarios [42] were developed using the global change assessment model (GCAM). The RCP 8.5 SSP-5 [43] and RCP 7.0 SSP-3 [44] scenarios were simulated using the regionalized model of investments and development—the model of agricultural production and its impact on the environment (REMIND—MAgPIE; [43]) and the Asia-Pacific integrated model (AIM; [44]), respectively. Land use change under RCP 4.5 SSP-2 scenario was simulated using MESSAGE-GLOBIOM model [45]. The RCP8.5 scenario represents business as usual (highest) global warming, whereas the lower RCPs signify mitigation scenarios with lesser predicted warming [12,13]. The SSPs are described as follows:

The SSP-1 (*sustainability—taking the green road*) scenario represents a world shifting towards a more sustainable path, characterized by healthy diets, low waste, reduced meat consumption, increasing crop yields, reduced tropical deforestation, and high trade, which, together collectively "respects the environmental boundaries" [41].

SSP-2 is a business-as-usual (*middle of the road scenario*) scenario characterized by development along historical patterns such that meat and food consumption converge slowly towards high levels, trade is largely regionalized, and crop yields in low-income regions catch up with high-income nations, but the land use change is incompletely regulated, with continued tropical deforestation (although at declining rates) [19,45].

The SSP-3 (*regional rivalry—a rocky road*) scenario represents a world with resurgent nationalism, increased focus on domestic issues, almost no land use change regulations, stagnant crop yields due to limited technology transfer to developing countries, and prevalence of unhealthy diets with high shares of animal-based products and high food waste [44].

In SSP-4 (*inequality—a road divided*), the disparities increase both across and within countries such that high-income nations have strong land use change regulations and high crop yields, while the low-income nations remain relatively unproductive with continued clearing of natural vegetation. Rich elites have high consumption levels, while others have low consumption levels [42].

The SSP-5 (*fossil fueled development—taking the highway*) scenario is characterized by rapid technological progress, increasing crop yields, global trade, and competitive markets, where unhealthy diets and high food waste prevail. There are medium levels of land use change regulations in place, meaning that tropical deforestation continues, although its rate declines over time [43].

2.2. Land Use Data

We downloaded the gridded maps from the LUH2 website [21] that provide the fraction of each of 12 land use types for each ($0.25° \times 0.25°$ resolution) cell for five separate points in time: past (850 and 1900), present (2015), and two future years (2050 and 2100). The 12 land use classes include 2 classes of primary undisturbed natural vegetation (forests, non-forests) and 10 human land uses (see Table 1). The 10 human land uses comprise two secondary (regenerating) vegetation land use classes (forest, non-forest), two grazing (pasture, rangeland), one urban, and five cropland (C3 annual, C3 permanent, C4 annual, C4 permanent, and C3 nitrogen fixing crops) uses. C3 and C4 correspond to temperate (cool) season crops and tropical (warm) season crops, respectively.

Table 1. Projected number of endemic species (Equation (1)) and phylogenetic diversity (Equation (4); phylogenetic diversity (PD) in million years (MY)) committed to extinction under past (850, 1900 AD), present (2015), and future (2050, 2100) land use extent (mean values). Supplementary Table S3 presents the 95% confidence interval for the estimates. M, B, A, and T correspond to mammals, birds, amphibians, and total, respectively. See methods for details on six climate mitigation (RCP) and socio-economic (SSP) scenario combinations.

Year	Scenario	Projected Endemic Extinctions				Projected PD Loss (MY)			
		M	B	A	T	M	B	A	T
850	Past	6	5	15	25	0	3	20	24
1900	Past	74	86	212	372	268	271	1137	1675
2015	Present	199	222	602	1023	948	828	3493	5270
2050	RCP2.6 SSP-1	219	236	665	1120	1039	872	3875	5787
	RCP4.5 SSP-2	239	255	720	1214	1155	952	4212	6319
	RCP7.0 SSP-3	249	260	746	1255	1202	976	4394	6572
	RCP3.4 SSP-4	267	270	764	1301	1338	1022	4517	6876
	RCP6.0 SSP-4	252	253	735	1241	1272	943	4391	6606
	RCP8.5 SSP-5	241	255	747	1244	1157	920	4421	6499
2100	RCP2.6 SSP-1	241	256	734	1232	1226	941	4293	6459
	RCP4.5 SSP-2	297	317	816	1430	1455	1230	4756	7441
	RCP7.0 SSP-3	302	301	883	1485	1523	1150	5203	7876
	RCP3.4 SSP-4	398	408	1035	1841	1997	1575	6100	9672
	RCP6.0 SSP-4	320	319	883	1522	1581	1203	5273	8057
	RCP8.5 SSP-5	278	281	825	1385	1365	1043	4878	7286

Next, we calculated the area of each land use type in each grid cell by multiplying the fractions with the total cell area. Finally, for each point in time (850, 1900, 2015, 2050, and 2100) and scenario, we calculated the area (km^2) of each of the 12 land classes in each of the 804 terrestrial ecoregions [26] by overlaying the area maps with ecoregion boundaries in ArcGIS.

2.3. Projecting Species Extinctions

For each year and scenario, we fed the estimated areas of each of 12 land use types into the countryside species–area relationship (SAR; [23]) to estimate the number of endemic species projected to go extinct $(Slost)$ as a result of total human land use within a terrestrial ecoregion j as follows [22]:

$$Slost_{g,j} = Send_{g,j} - Send_{g,j} \cdot \left(\frac{Anew_j + \sum_{i=1}^{10} h_{g,i,j} \cdot A_{i,j}}{Aorg_j} \right)^{z_j} \tag{1}$$

Here, $Send_{g,j}$ is the number of endemic species of taxon g (mammals, birds, amphibians) in ecoregion j, $Aorg_j$ is the total ecoregion area, $Anew_j$ is the remaining natural habitat area in the ecoregion (primary vegetation forests + primary vegetation non-forests), $h_{g,i,j}$ is the affinity of taxon g to the land use type i in the ecoregion j (which is based on the endemic species richness of the taxon in that land use type relative to their richness in natural habitat), $A_{i,j}$ is the area of a particular human land use type i (total of 10), and z_j (z-value) is the SAR exponent. The exponent z is the slope of the log–log plot of the power-law SAR describing how rapidly species are lost as habitat is lost [46]. Note that the classic SAR is a special case of the countryside SAR, when $h = 0$.

Following Chaudhary and Brooks [22], we obtained the numbers of endemic species of each taxon per ecoregion ($Send_{g,j}$) from the International Union of Conservation of Nature (IUCN) species range maps [14], z-values (z_j) from Drakare et al. [46], and the taxon affinities ($h_{g,i,j}$) to different land use types from the habitat classification scheme database of the IUCN [25]. This database provides information on the human land use types to which a particular species is tolerant to and within which it has been observed to occur. Each land use and habitat is coded either 'suitable' (i.e., when the species occurs frequently or regularly), 'marginal' (i.e., when the species occurs in the habitat only infrequently or only a small proportion of individuals are found there), or 'unknown'. In this study, we considered a species to be tolerant to human land use only if it is coded as 'suitable' for that species. This way, we might have overestimated the projected biodiversity loss. Regardless, these are the best data available for parameterizing the countryside SAR on a global scale.

For example, through the IUCN habitat classification scheme [25], one can look up that House Sparrow (*Passer domesticus*) is tolerant to all human land use types (http://www.iucnredlist.org/details/classify/103818789/0); the frog *Callulops comptus* is tolerant to degraded forests, but not to any other human land use type (http://www.iucnredlist.org/details/classify/57731/0); but *Cophixalus nubicola* can only survive in primary (undisturbed) forests and grasslands (http://www.iucnredlist.org/details/classify/57781/0) and not in any human-modified landscape [25].

For each of the 804 ecoregions, we counted the number of endemic species per taxon that are tolerant to the human land use type i and divided this by the total number of endemic species of that taxon occurring in the ecoregion, in order to obtain the fractional species richness. Supplementary Table S1 lists how we matched each of the 10 human land use classes of the LUH2 [21] with the six land use classes of IUCN habitat classification scheme [25].

The affinity of taxonomic group g to the land use type i is then calculated as the proportion of all species that can survive in it (fractional richness), raised to the power $1/z_j$ [22,23]. Therefore, the taxon affinity estimate ($h_{g,i,j}$) is high in ecoregions hosting a high number of species tolerant to human land uses, but low in ecoregions comprising of species that cannot tolerate human land uses. We derived the 95% confidence intervals for projected species extinctions in each ecoregion by considering uncertainty in the z-values (z_j) [46]. See Supplementary Table S1 for further details and sources of all model parameters.

In order to validate the current predicted number of species (in 2015) committed to extinction per ecoregion by the parameterized model, we compare them with the documented ("observed") number of ecoregionally endemic species currently listed as threatened with extinction (i.e., those with threat status of critically endangered, endangered, vulnerable, extinct in wild, or extinct) on the 2015 IUCN Red List [14]. Supplementary Table S2 and Chaudhary and Brooks [22] present further details on validation procedure.

We used Equation (1) to calculate the number of species committed to extinction ($Slost_{g,j}$) in each ecoregion due to human land use extent in five different years: 850, 1900, 2015, 2050, and 2100 (T1 to T5). We then derived the number of additional projected extinctions for the four periods: (850–1900), (1900–2015), (2015–2050), and (2015–2100), by subtracting $Slost_{g,j}$ at T1 from $Slost_{g,j}$ at T2, and so on.

In addition to absolute projected species loss numbers, we also calculated the rate of projected species loss per taxon for these four time periods by dividing additional extinctions with the time interval and the total species richness (i.e., both endemic and non-endemic) of the taxon ($Sorg_g$).

$$(\mathrm{E/MSY})_{g,\ T1-T2} = \frac{10^6 \cdot \left(Slost_{g,T2} - Slost_{g,T1}\right)}{Sorg_g \cdot (T2 - T1)} \tag{2}$$

The rate of projected species loss unit is projected as extinctions per million species years (E/MSY), representing the fraction of species going extinct over time. We note that this definition of rate of species loss is different than the traditional definition, in that it includes both species going extinct as well as additional species committed to extinction (extinction debt) over the time interval. The traditional definition only considers the extinctions that have been materialized in the time period and does not include the extinction debt.

2.4. Projecting Evolutionary History Loss

We projected the loss of phylogenetic diversity in each ecoregion in three steps. First, we obtained the evolutionary distinctiveness (ED) scores for all species of birds, mammals, and amphibians from

Chaudhary et al. [37]. Next, for each ecoregion j, we used a MATLAB routine to sum the ED scores for m randomly chosen endemic species from that ecoregion:

$$EDloss_{g,j} = \sum_{k=1}^{m} ED_{k,g,j} \tag{3}$$

Here, m is the projected species loss as calculated by the countryside SAR for ecoregion j and associated taxa g in Equation (1) (i.e., $m = Slost_{g,j}$). We repeated this 1000 times through Monte Carlo simulation and used the mean and 95% confidence interval of the cumulative ED lost (in million years) per ecoregion. Note that the species ED scores are global (i.e., one ED score for one species) and not ecoregion-specific.

Finally, we use the least-squares slope (s_g) of the linear model (derived by Chaudhary et al. [37]), describing the tight relationships ($R^2 > 0.98$) between ED loss versus PD loss for each of the three taxa to convert cumulative ED loss per ecoregion to PD loss per ecoregion for a given taxon (Equation (4)). The linear slope (s_g) values used for mammals, birds, and amphibians are 0.51, 0.61, and 0.46, respectively [37].

$$PDloss_{g,j} = EDloss_{g,j} \times s_g \tag{4}$$

Further details and discussion on the above approach can be found in Chaudhary et al. [37]. Similar to the rate of species loss (Equation (2)), we also calculated the rate of PD loss in the units million years lost per million phylogenetic years (MY/MPY):

$$(\mathrm{MY/MPY})_{g,\ T1-T2} = \frac{10^6 \cdot \left(PDloss_{g,T2} - PDloss_{g,T1}\right)}{PDtotal_g \cdot (T2 - T1)} \tag{5}$$

2.5. Drivers of Evolutionary History Loss in Each Ecoregion

The projected species extinctions and PD lost per ecoregion is then allocated to the different land use types i according to their area share $A_{i,j}$ in the ecoregion j and the affinity $(h_{g,i,\ j})$ of taxa to them. The allocation factor $a_{g,i,j}$ for each of the 10 human land use types i (such that for each ecoregion j, $\sum_{i=1}^{10} a_i = 1$) is as follows [22,27,28]:

$$a_{g,i,\ j} = \frac{A_{i,\ j} \cdot (1 - h_{g,\ i,\ j})}{\sum_{i=1}^{10} A_{i,\ j} \cdot (1 - h_{g,\ i,\ j})} \tag{6}$$

The contribution of different land use types towards the total PD loss in each ecoregion is then given by the following [37]:

$$PDloss_{g,j,i} = PDloss_{g,j} \times a_{g,i,\ j} \tag{7}$$

Equation (7) thus provides the projected PD loss (MY) caused by a particular land use in a particular ecoregion. Replacing $PDloss_{g,j}$ with $Slost_{g,j}$ provides the contribution of each land use type to total species extinctions per ecoregion [22]. We also calculate the projected extinctions and *PDloss* for each of 176 countries based on the share of ecoregion and different land use types within them [22,27,28].

3. Results

3.1. Future Natural Habitat Loss

Across all six coupled RCP-SSP scenarios, an additional 5.87–11.77 $\times$ 10^6 km^2 of natural vegetative cover is projected to be lost between 2015 and 2050 to make way for human land uses, equivalent to 10–20% of total remaining area of natural vegetation across all ecoregions in 2015. From 2050–2100, a further 5.4–12.1 $\times$ 10^6 km^2 natural vegetation loss is projected, depending upon the scenario. Among the six scenarios, RCP 2.6 SSP-1 projected the least loss of natural vegetative cover, followed by RCP 8.5 SSP-5, RCP 4.5 SSP-2, RCP 7.0 SSP-3, and RCP 6.0 SSP-4. The scenario with second most stringent climate mitigation target, which is coupled with a less benign shared social pathway (RCP 3.4 SSP-4), projected the greatest loss of natural vegetative cover (24 million km^2 between 2015–2100).

Secondary vegetation (e.g., logged forests) will be responsible for the conversion of the majority of natural vegetation area from 2015–2100, followed by conversion to cropland. While currently in 2015, the combined area of pasture and rangelands for livestock grazing constitutes the most dominant human land use, all six scenarios project that by 2100, secondary vegetation will be most dominant human land use type globally. The RCP2.6 SSP-1 and RCP8.5 SSP-5 both project abandonment of grazing area from 2015–2100 (with subsequent increases in secondary vegetation), while the other four scenarios project a marginal increase.

Compared with other four scenarios, the two most stringent climate scenarios (RCP2.6 SSP-1 and RCP3.4 SSP-4) entail a large increase in C3 and C4 permanent crop area (5 million km^2 and 16 million km^2, respectively) compared with current levels.

3.2. Projected Species Richness and Evolutionary History Loss

As shown in Table 1, we found that a total of 1023 endemic species (199 mammals, 222 birds, and 602 amphibians) are committed to extinction (or have gone extinct) as a result of land use change to date (2015). The 95% confidence interval, taking into account the uncertainty in the slope of the countryside species–area relationship (z-values; [22]), is 958–1113 projected endemic extinctions globally (Supplementary Table S3).

This number is equivalent to ~30% of all endemic species across all ecoregions and corresponds to a projected loss of 5270 million years (MY) of phylogenetic diversity (95% confidence interval: 3912–6967 MY) across the three taxa. The taxonomic breakdown is 948, 828, and 3493 MY of phylogenetic diversity (PD) loss for mammals, birds, and amphibians, respectively. Compared with inferences for 850 and 1900, the current total represents a three-fold increase in number of species and evolutionary history committed to extinction globally (Supplementary Table S3).

Our projected species extinctions as a result of current land use extent (2015) for each taxon per ecoregion compare well with the number species documented as threatened with extinction (i.e., those with threat status of critically endangered, endangered, vulnerable, extinct in wild, or extinct) by the IUCN Red List in 2015 [14], with correlation coefficients of 0.74, 0.75, and 0.85 for mammals, birds, and amphibians, respectively (see Table S2 in supporting information for goodness-of-fit values and additional notes).

As a consequence of further natural land clearing and land use changes from 2015–2100, we project that an additional 209–818 endemic species will be committed to extinction by 2100 (Table 1). The concomitant PD committed to extinction amounts to 1190–4402 million years. Compared with mammals and birds, a three times higher loss of amphibian species is projected owing to their small range and high level of endemism. Also, owing to higher evolutionary distinctiveness scores (ED score in MY, [37]) of amphibians, the projected PD loss of amphibians per unit projected species extinction is relatively higher than that of mammals and birds (Table 1). The highest biodiversity loss as a result of land use change is projected to occur under the RCP3.4 SSP-4 scenario, followed by RCP6.0 SSP-4, RCP7.0 SSP-3, RCP4.5 SSP-2, and RCP8.5 SSP-5 (Table 1). The RCP2.6 SSP-1 scenario is projected to result in least number of additional species and PD committed to extinction by 2100 as a result of land use change.

Interestingly, we found that even under the similar socio-economic trajectory (SSP-4), the impacts may vary within a region as a result of land use changes that are driven by climate mitigation efforts such as replacing fossil fuels with biofuels (RCP3.4 vs. RCP6.0). While the land use change by 2100 in more stringent climate scenario (RCP3.4) is projected to commit an additional 818 species to extinctions compared with 2015 levels, the corresponding number for RCP 6.0 is 499 (Table 1). The difference between these two scenarios is primarily because of an expansion of C3 and C4 permanent crop area in Southeast Asia and Mexico for biofuel purposes under the RCP3.4 scenario (Supplementary Table S7).

3.3. Land Use Drivers of Biodiversity Loss

Table 2 shows the contribution of 10 human land use types to the total projected biodiversity loss (mammals, birds, and amphibians combined) in the past, present, and future, calculated through allocation factor ($0 \leq a_{g,i,\,j} \leq 1$) in Equations (6) and (7) (methods). Currently in 2015, the global secondary vegetation (forests + non-forests), grazing land (pasture + rangeland), and cropland are responsible for committing 378, 333, and 289 species (37%, 33%, and 28%) of the total 1023 projected extinctions, respectively.

Table 2. Contribution of different human land use types (in %; Equations (6) and (7)) to total number of species and phylogenetic diversity (mammals, birds, and amphibians combined) committed to extinction in the past (850, 1900 AD), present (2015), and future (2100) under six climate mitigation (RCP) and socio-economic (SSP) scenario combinations *.

Land Use Type	Past		Present	% of Total Projected Extinctions in 2100AD					
	850 AD	1900 AD	2015 AD	RCP2.6 SSP-1	RCP2.6 SSP-2	RCP7.0 SSP-3	RCP3.4 SSP-4	RCP6.0 SSP-4	RCP8.5 SSP-5
Sec. Veg. (forests)	0	28	28	35	35	28	21	30	35
Sec. Veg. (non-forests)	0	19	9	13	11	8	8	8	11
Pasture	7	13	21	11	13	17	15	20	16
Rangeland	44	16	11	8	7	10	8	10	8
Urban	0	0	2	3	3	3	3	4	3
C3 annual crops	20	9	11	9	12	13	11	11	10
C3 permanent crops	13	7	9	11	10	10	13	8	8
C4 annual crops	9	4	5	3	5	6	4	4	6
C4 permanent crops	2	1	1	5	1	1	13	3	1
C3 Nitrogen fixing crops	4	2	2	2	3	3	2	2	3

* Note that the contribution % remains the same for both metrics (species extinctions and evolutionary history) because the same allocation factor is used (Equation (6)).

By 2100, the contribution of grazing area to total extinctions is projected to decrease to 19–30% depending upon the scenario, while secondary vegetation will be responsible for the majority of projected extinctions under five out of six scenarios (Table 2). The exception is the SSP-4 RCP3.4 scenario, where agriculture land (particularly C3 and C4 permanent crop area) is projected to be the most damaging land use type, contributing to 48% of all projected extinctions in 2100.

3.4. Rates of Biodiversity Loss

We found that for all three taxa combined, the current projected rate (over the period 1900–2015) of endemic species committed to extinction is 242 extinctions per million species years (E/MSY; Equation (2)), which is ~20 times higher than the inferred past rate (850–1900) of projected extinctions (Figure 1a). The 95% confidence interval is 228–261 E/MSY.

The rate of current phylogenetic diversity (PD) loss is 156 (95% confidence interval: 124–185) million years per million phylogenetic years (MY/MPY; Equation (5), also ~20 times higher than the past rate of 8 MY/MPY (Figure 1b)). Amphibians have the highest rates of loss (515 E/MSY, 289 MY/MPY), followed by mammals (192, 120) and birds (106, 60). Supplementary Table S3 presents the taxon-specific (mammals, birds, and amphibians) rates of projected extinctions for past, present, and future.

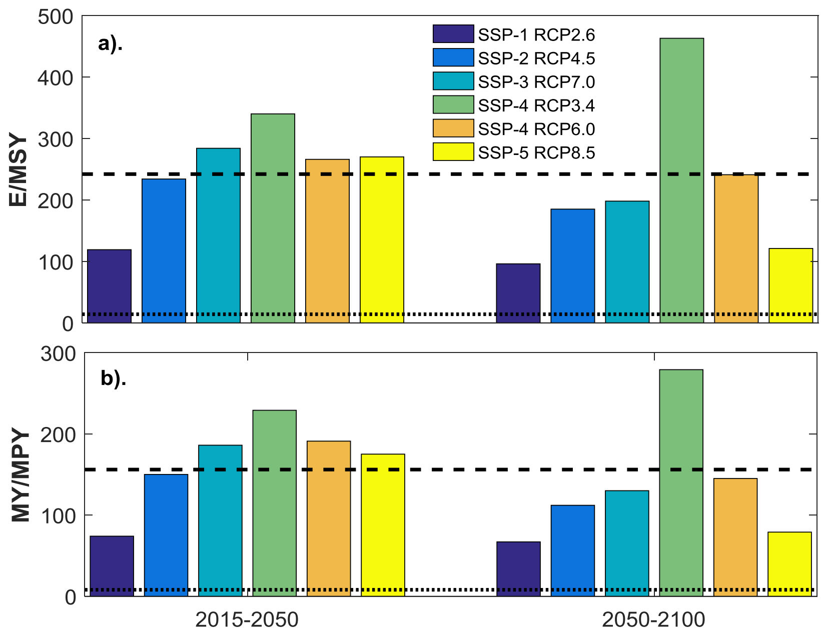

Figure 1. Past, present, and future rates of projected biodiversity loss. Future rate of biodiversity loss (mammals, birds, and amphibians combined) in projected endemic species extinctions per million species years (**a**) and projected PD loss per million phylogenetic years (**b**) under six climate mitigation (RCP) and socio-economic (SSP) scenario combinations. For comparison, past (850–1900) rate of loss is represented by the dotted line and current (1900–2015) rate of loss is shown by a dashed line. See Supplementary Table S3 for taxon-specific (amphibians, mammals, birds) rates of loss along with the 95% confidence intervals for the estimates.

The rate of biodiversity loss is projected to increase as a result of land use change for the period 2015–2050 under all scenarios but one; under the combination of the lowest climate forcing (RCP2.6) and the most benign developmental path (SSP-1), the rate of biodiversity loss is expected to reduce to half its current level. This projected amelioration extends to three other scenarios over the period 2050–2100; compared with the 2015–2050 period, we found a reduction in land use change driven rate of biodiversity loss in the second half of the century of 149 E/MSY, 86 E/MSY, and 49 E/MSY under the RCP8.5 SSP-5, RCP7.0 SSP-3, and RCP4.5 SSP-2 scenarios, respectively (see Figure 1).

However, no such reduction is projected for the RCP3.4 SSP-4, which represents the worst case outcome for land use change driven biodiversity loss. Here, an additional 818 species are committed to extinction globally by 2100 (representing 4402 MY of PD) compared with 2015 levels—twice the current level and ~1.5 times the rate in the 2015–2050 period (see Figure 1). This is primarily due to this SSP's predicted major expansion of C3 and C4 permanent crop area (Table 2) in tropical and subtropical ecoregions.

3.5. Hotspots of Biodiversity Loss

Figure 2a shows the current hotspot ecoregions where the land use change to date is projected to cause high amounts of PD loss (Equation (4)). These ecoregions span Madagascar, Eastern arc forests (Kenya, Tanzania), northwest Andes (Central Colombia), Appalachian Blue Ridge forests (eastern USA), Peruvian Yungas, Bahia coastal forests (Eastern Brazil), and Palawan forests (Philippines).

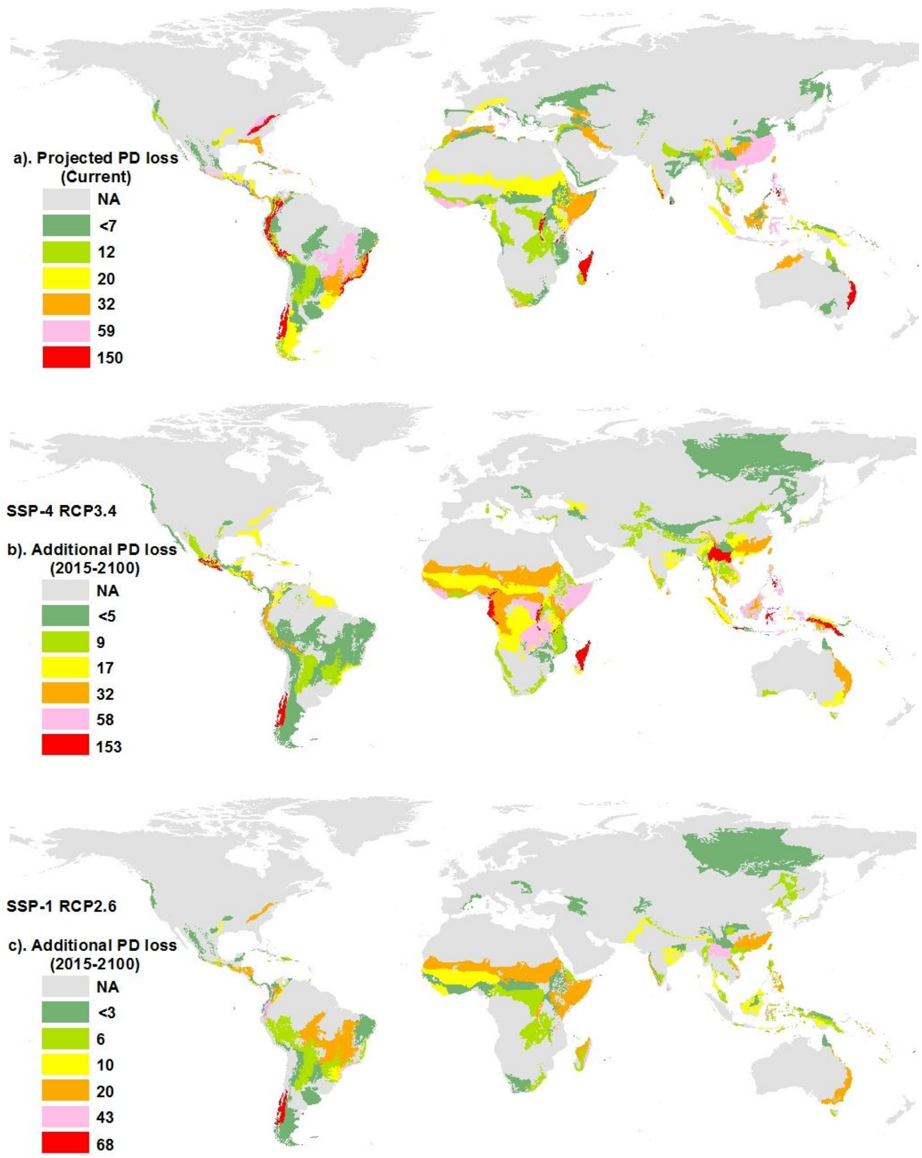

Figure 2. Hotspots of phylogenetic diversity (PD) loss under current and future human land use extent. (**a**). Projected loss of PD in millions of years (MY) associated with projected endemic species extinctions (mammals, birds, and amphibians combined) as a result of current (2015) human land use in each of 804 terrestrial ecoregions, (**b**). Additional PD (in MY) committed to extinction as a result of land use change under RCP3.4 SSP-4 scenario (worst case) in the period 2015–2100, (**c**). Additional PD (in MY) committed to extinction as a result of land use change under RCP2.6 SSP-1 scenario (best case) in the period 2015–2100. NA—not applicable (no endemics in the ecoregion).

We found that hotspots of projected species loss do not always overlap with hotspots of projected PD loss. For example, while currently (year 2015), the Appalachian forest ecoregion in eastern USA ranks 11th among the 804 ecoregions in terms of projected species loss (15 extinctions), it ranks 4th in terms of projected PD loss (113 MY), because of its harboring of many old endemic amphibian lineages. The Spearman rank correlation coefficient between the species and PD loss estimates was found to be 0.77, 0.77, and 0.85 for mammals, birds, and amphibians, respectively.

Conversely, the Comoros forest ecoregion between Madagascar and East Africa ranks 4th in terms of projected species loss (22 extinctions), but 19th for PD loss—here, endemic species are relatively young. Figure 2b shows the additional PD loss per ecoregion due to future land use change (2015–2100) under the worst-case RCP3.4 SSP-4 scenario. Most current hotspots of species and PD loss, such as Madagascar and Eastern arc forests, are projected to continue losing the biodiversity under this scenario. However, other current hotspots of loss, such as the Appalachian forests (USA) and the Bahia forest (Brazil) ecoregions, are not expected to experience significant land use change, and hence no additional biodiversity loss is projected under this scenario.

Importantly, as a result of clearing of natural vegetation under the RCP3.4 SSP-4 scenario, new hotspots of global species and PD loss emerge, that is, ecoregions that have hitherto been relatively undamaged from human land use. This includes Sulawesi montane forests (Indonesia), Cameroonian highland forests, and central range montane forests (Papua New Guinea, Indonesia), each with an additional 20–30 projected species loss and around 100 MY of additional PD loss (Figure 2b). Supplementary Table S4 presents the additional species and PD loss in each of 804 ecoregions under all future scenarios.

We found that hotspots of future biodiversity loss differ depending upon the scenario. For example, while the RCP3.4 SSP-4 scenario projects an additional 11 MY of PD loss in Serra do Mar forest ecoregion in eastern Brazil over the period 2015–2100, the projected loss is three times higher (34 MY) under the RCP2.6 SSP-1 scenario. Conversely, unlike RCP3.4 SSP-4, the RCP2.6 SSP-1 scenario projects almost no additional biodiversity loss in Cameroonian highland or central range forest ecoregions.

The hotspots of future biodiversity loss also differ depending upon the taxon. For example, under the worst case for biodiversity scenario (RCP3.4 SSP-4), the ecoregion with highest number of projected additional endemic mammal species extinctions (over 2015–2100) is the Sulawesi rain forest ecoregion in Indonesia. The Galapagos Island ecoregion is projected to bear the most additional bird species extinctions, while the Madagascar lowland forests will see the most amphibian species extinctions.

We also calculated the projected biodiversity loss for each of the 176 countries, as well as the contribution of each land use type to total projected loss in each nation under all future scenarios. Supplementary Table S5 presents the additional biodiversity loss in each country and supplementary Tables S6 and S7 present the biodiversity loss allocated to each of the 10 land use types in each country under all future scenarios. Table 3 shows the additional biodiversity loss projected for seven World Bank regions under six future scenarios (derived by summing up the projected species and PD loss estimate for all countries within a region). As expected, the majority of future biodiversity loss is projected to occur as a result of land use change in tropical countries with a high endemism per unit area.

The projected biodiversity loss is small in North America, Europe and Central Asia (EU&CA), and the Middle-East and North Africa (MENA), regardless of scenario (Table 3), while the amount of biodiversity loss in the other four regions differs depending upon the scenarios. For example, in the period 2015–2050, the RCP7.0 SSP-3 scenario projects the highest land use change driven endemic extinctions in Sub-Saharan Africa (SSA), while the RCP3.6 SSP-4 projects the highest losses in East Asia and the Pacific (EAP), and the RCP8.5 SSP-5 scenario highlights Latin America and the Caribbean (LAC; Table 3). In terms of country level numbers, while RCP3.6 SSP-4 projects just five additional endemic species committed to extinction in Brazil between 2015–2100, the corresponding additional extinctions under RCP8.5 SSP-5 is very high at 42 (Supplementary Table S5).

These varying results also reflect the temporal trajectories of land use change in a particular region under a specific scenario. For example, the RCP8.5 SSP-5 scenario projects almost similar biodiversity loss in LAC (Latin America and the Caribbean) and SSA (Sub-Saharan Africa) for the period 2015–2050, but projects substantially higher loss in EAP (East Asia and the Pacific) in the period 2050–2100 than the other two regions.

Finally, hotspots of future biodiversity loss also differ depending upon the metric of biodiversity loss. For example, between 2015–2050, the most optimistic RCP2.6 SSP-1 scenario would commit the East Asia and the Pacific (EAP) region to the greatest number of endemic species extinction, whereas Latin America and the Caribbean (LAC) emerges as the region projected to lose the most additional PD (see bold numbers in Table 3). Here, as before, the difference is driven mainly by the higher numbers of older, endemic amphibians in Latin America.

Table 3. Additional number of endemic species richness (SR) and phylogenetic diversity (PD in millions of years) committed to extinction (for mammals, birds, and amphibians combined) in seven World Bank regions * for the periods 2015–2050 and 2050–2100 as a result of land use change under six coupled climate mitigation (RCP) and socio-economic (SSP) scenarios. Bold figures represent the regions with highest projected loss for a particular scenario. See Supplementary Table S5 for country-specific numbers under each scenario.

Metric	Period	Scenario	EAP	EU&CA	LAC	MENA	N. America	S. Asia	SSA
SR	2015–2050	SSP-1 RCP2.6	**30**	0	28	0	3	14	13
		SSP-2 RCP4.5	60	2	**68**	1	3	22	34
		SSP-3 RCP7.0	58	0	59	0	3	27	**77**
		SSP-4 RCP3.4	**96**	0	49	0	4	32	88
		SSP-4 RCP6.0	55	0	40	0	4	27	**82**
		SSP-5 RCP8.5	50	0	**66**	0	3	29	62
	2050–2100	SSP-1 RCP2.6	**45**	1	41	0	2	8	17
		SSP-2 RCP4.5	**176**	6	110	2	4	26	79
		SSP-3 RCP7.0	65	2	63	0	1	3	**95**
		SSP-4 RCP3.4	**281**	7	100	1	1	7	137
		SSP-4 RCP6.0	101	4	42	2	0	6	**127**
		SSP-5 RCP8.5	**65**	3	31	0	1	4	43
PD	2015–2050	SSP-1 RCP2.6	139	5	**167**	0	16	117	73
		SSP-2 RCP4.5	314	13	**368**	2	14	153	187
		SSP-3 RCP7.0	257	16	338	1	16	184	**482**
		SSP-4 RCP3.4	535	10	281	1	23	206	**544**
		SSP-4 RCP6.0	330	5	268	1	24	186	**518**
		SSP-5 RCP8.5	286	5	**363**	1	15	203	354
	2050–2100	SSP-1 RCP2.6	**269**	0	232	1	10	27	130
		SSP-2 RCP4.5	**884**	31	597	2	23	175	446
		SSP-3 RCP7.0	403	8	335	1	2	6	**557**
		SSP-4 RCP3.4	**1358**	44	513	1	12	50	784
		SSP-4 RCP6.0	494	28	179	1	2	26	**695**
		SSP-5 RCP8.5	**306**	23	169	0	1	8	275

* The seven World Bank regions are the following: East Asia and the Pacific (EAP), Europe and Central Asia (EU&CA), Latin America and the Caribbean (LAC), Middle-East and North Africa (MENA), North America, South-Asia, and Sub-Saharan Africa (SSA).

4. Discussion

The large variations in the magnitude and location of projected land use changes and the consequent biodiversity outcomes across different SSP-RCP scenarios and across taxa (Tables 1–3; Figures 1 and 2; Supplementary Tables S3–S6) are a result of the complex interplay of mitigation measures adopted to achieve the climate target under a particular RCP [12], the integrated assessment model used for simulation [11], the future socio-economic conditions under each SSP (e.g., land use change regulations, food demand, dietary patterns, global trade, technological change in agriculture sector, etc. [17,19]) and the biodiversity theatre on which all this plays out.

The ambitious RCP2.6 SSP-1 scenario is projected to result in lowest land use change driven global biodiversity loss. The RCP 2.6 target would be achieved by the deployment of bioenergy (C4 permanent) crops in conjunction with carbon capture and storage technology [40]. While this does entail clearing of some natural habitat and therefore some biodiversity loss, the demand for agricultural products is lowest among the SSPs, due to lower projected population growth, adoption of sustainable food consumption practices, and an increase in agricultural yields and global trade [19,41]. These SSP factors outweigh the natural habitat clearing needed to achieve RCP2.6 climate mitigation target, with the net result being relatively low biodiversity loss.

In contrast, the SSP-4 RCP 3.4 (the worst case scenario for projected land use change driven biodiversity loss) has the climate mitigation measures (deployment of bioenergy crops) and SSP factors (high population growth, lower crop yields, and weak land use change regulation in the tropical countries, [42]) working synergistically and leading to large amounts of natural habitat loss in biodiversity hotspots, and consequent biodiversity loss. The RCP6.0 SSP-4 performs better than the RCP3.4 counterpart because the less ambitious climate target necessitates relatively low levels of bioenergy crop expansion.

The RCP8.5 SSP-5 scenario showed the second lowest biodiversity loss despite being characterized by high food waste and diets high in animal-source food. This is because of an absence of any explicit climate mitigation efforts that result in land use change, and in addition, a strong increase in crop yields, global trade, and medium levels of land use change regulation [43]. In particular, the land demand and rate of biodiversity loss is substantially reduced in the second half of the century (Figure 1) as the population decreases, consumption levels stabilize, and livestock production shifts from extensive to more intensive animal husbandry systems [43]. However, our extinction projections do not include losses due to the direct effects of climate change—it may be that the increased global forcing of RCP8.5 counteracts any biodiversity savings due to SSP-5 driven habitat sparing (see below).

Among the six scenarios, RCP7.0 SSP-3 ranks in the middle for biodiversity losses. As the climate mitigation target is not very stringent, the land use change due to bioenergy crop expansion is low. However, socio-economic (SSP-3) factors, such as continued high demand for agricultural and animal based products, low agricultural intensification and low trade levels, and no regulations on tropical deforestation, lead to high increase in pasture and cropland areas for food and feed production [44]. This cascades into high losses of natural vegetation and endemic species extinctions.

The application of countryside SAR allowed us to allocate the total projected loss to individual land use types (Equations (6) and (7); Table 2 and Table S6). All future scenarios show an increase in secondary vegetation area at the cost of the natural habitat primarily to meet the increasing wood demand [9]. We found that this leads to substantial biodiversity loss in all six scenarios (Table 2), indicating that, regardless of climate mitigation, sustainable forest management will be critical for future biodiversity conservation. This lends support to the call for low-intensity wood harvesting techniques, such as reduced impact logging, to protect biodiversity (see, e.g., [15]).

Another important factor that has negative consequences for global biodiversity is the deployment of biofuel crops in tropical countries as a part of climate mitigation strategy. For example, unlike the RCP6.0 SSP-4 scenario, a high increase in permanent crop area for biofuel production is projected in Papua New Guinea under RCP3.6 SSP-4 over the period 2015–2100. This increase in permanent crop area alone is projected to commit an additional 29 species in that area to extinction (Supplementary Table S7).

We could only account for the uncertainty in SAR exponent (z-values) and not for other model parameters, owing to lack of uncertainty information in the underlying data such as species presence [14] or land use area [21]. Our projections of biodiversity loss are conservative for several reasons. First, the SAR approach we use cannot quantify instances where the land use change wipes out the habitat of non-endemic species from all the ecoregions in which they occur [22]. Second, we only considered the species loss for three taxa (mammals, birds, and amphibians) for which necessary data were available for this analysis, and we do not know how to scale patterns from these three taxa to biodiversity in general. Third, and importantly, we did not include direct climate-change driven extinctions. In contrast, we might have overestimated the projected loss due to our use of the IUCN habitat classification scheme ([25], see methods). We could not account for ecosystem services disruption (e.g., destruction of mutualistic relationships, such as pollination or seed dispersal) and interdependence among species (e.g., mesopredator release) that can affect biodiversity loss through cascading changes.

We selected the species randomly and summed their ED scores to arrive at the PD loss (Equation (3)). However, future studies could further constraint the random loss scenario by first selecting the species most at risk of extinction (e.g., those with IUCN threat status of critically endangered, endangered, vulnerable). However, this is expected to not change the projected PD loss numbers substantially because previous studies have found no significant positive relationship between ED scores and IUCN risk, that is, threatened species do not have systematically higher or lower ED scores than non-threatened species (see Jetz et al. [31] and Chaudhary et al. [37] for discussion).

The scope of our study mirrors that of Jantz et al. [9], who also quantified the potential extinctions in biodiversity hotspots under future land use change scenarios, but did not model the climate change effects. However, climate change can degrade currently suitable habitats, can shift suitable habitats to areas that cannot be reached, and can produce unsuitable or unavailable climate envelopes, all which can threaten species directly, driving them towards extinction [47,48], and several studies have demonstrated that climate-change will exacerbate the impact of habitat loss on species [49–52]. However, the relative additive and interactive contributions of direct and indirect effects are not yet fully known.

Van Vuuren et al. [8] found that, compared with land use change, climate change is expected to contribute three times less to vascular plant diversity loss on a global scale. A recent review by Titeux et al. [7] found that while >85% of mammals, birds, and amphibian species listed as threatened with extinction on the IUCN Red List [14] are affected by habitat loss or degradation due to land use/cover change, just under 20% are affected by climate change. Climate change is a threat to only 7.1% of the vertebrate populations included in the Living Planet Index [53], while habitat loss or degradation constitutes an on-going threat to 44.8% of the populations [7].

That said, modelled species loss estimates in each ecoregion should generally be higher if the direct effects of climate change on species extinction risk are included [8,49]. For example, Mantyka-Pringle et al. [50] used a meta-analytic approach to detect where climate change might interact with habitat loss and fragmentation to negatively impact biodiversity. They showed that such negative interactions were most likely in regions with declining precipitation and high maximum temperatures. They found that the strength of the impact varied little across taxa, but varied across different vegetation types. Segen et al. [49] then applied this approach to identify ecoregions where such interaction is most likely to cause adverse impacts on biodiversity in future. Consequently, depending on the relative import of direct versus indirect effects of climate change, the ranking of the five more extreme climate change scenarios for biodiversity loss as reported here might change.

Explicitly integrating the two drivers is possible. Past studies have applied bioclimatic envelope models [53] to estimate loss of species habitat range due to climate change [51] and applying species–area relationship to translate this into projected extinctions [47,48]. Currently, this approach is limited to species whose range is sufficiently large or well-sampled enough to obtain an adequate sample of presence points for fitting bioclimatic envelope models (e.g., the authors of [51] could only include 440 species in their global analysis vs. the roughly 3400 species considered in our study here). Alternative approaches to assess species vulnerability to climate change based on correlative, mechanistic, or trait-based methods have been proposed (each with their strengths and weaknesses—reviewed in the literature [54]). However, we cannot quantify impacts on all species of multiple taxa at a global scale without much more underlying data, nor, given inherent uncertainties, can we assess the reliability of the projected impacts [54].

Clearly, including additional drivers such as climate change, habitat fragmentation [55], overexploitation/hunting, invasive species, and pollution would likely increase all biodiversity loss estimates [6], and perhaps in a differential manner under the various SSPs.

Overall, our results corroborate previous findings that land use change over coming decades is expected to cause substantial biodiversity loss. For example, Van Vuuren et al. [8] used four millennium ecosystem assessment scenarios [56] and projected that habitat loss by year 2050 will result in a loss of global vascular plant diversity by 7–24% relative to 1995 using the classic form of the species area–relationship model [57]. Jetz et al. [58] found that at least 900 bird species are projected to suffer >50% range reductions by the year 2100 due to climate and land cover change under four millennium ecosystem assessment scenarios. Jantz et al. [9] applied the classic (i.e., not correcting for habitat use) species–area relationship model [57] to gridded land use change data associated with four RCP scenarios (without the SSPs, [10]) and found that by 2100, an additional 26–58% of natural habitat will be converted to human land uses across 34 biodiversity hotspots and as a consequence, about 220 to 21,000 additional species (plants, mammals, birds, amphibians, and reptiles) will be committed to extinction relative to 2005 levels. More recently, Newbold et al. [59] used four RCP scenarios (again without the SSPs) and generalized linear mixed effects modeling to project that local plot-scale species richness will fall by a further 3.4% from current levels globally by 2100, under a business-as-usual land-use scenario; with losses concentrated in low-income, biodiverse countries. Unlike the above studies, one advantage of our use of countryside SAR is that it accounts for the fact that some species can survive in human land uses.

This study is the first, to our knowledge, to estimate potential future land use change driven terrestrial vertebrate biodiversity loss through two indicators (species richness and phylogenetic diversity) across all ecoregions and countries. We leveraged the IUCN habitat classification scheme [25] to parameterize the countryside species–area relationship model (SAR, [22]) that takes into account the information on how many species are tolerant to a particular land use type within an ecoregion [25]. The results show that the current rate (1900–2015) of projected biodiversity loss is ~20 times the past rate (850–1900) and is set to first increase in the period 2015–2050 under all scenarios (except under RCP2.6 SSP-1), and then decrease to levels below the current rate in the period 2050–2100 (expect under RCP3.4 SSP-4).

We found that out of the six future scenarios, the most aggressive one in terms of climate change mitigation effort (RCP2.6 SSP-1) is also the one projected to result in lowest land use change driven global biodiversity loss because of adoption of a sustainable path to global socio-economic development. However, the poor performance of the RCP3.4 SSP-4 scenario relative to RCP6.0 SSP-4 demonstrates that strategies to mitigate climate change (e.g., replacing fossils with fuel from bioenergy crops) can result in adverse global biodiversity outcomes if they involve clearing of natural habitat in the tropics.

Even in the best case RCP2.6 SSP-1 scenario, more than 10 million km^2 of primary habitat is projected to be converted into secondary vegetation for wood production or into permanent crops for bioenergy production in species-rich countries (Brazil, Colombia, Ecuador, Mexico, China, Sri Lanka) by the year 2100, potentially committing an additional 200 species and 1000 million years (MY) of evolutionary history to extinction (Supplementary Table S7). This implies that if we accept the importance of biodiversity to human well-being [60], then even a dramatic shift towards sustainable pathways such as healthy diets, low waste, reduced meat consumption, increasing crop yields, reduced tropical deforestation, and high trade, for example, as specified under the RCP2.6 SSP-1 scenario, is not likely not enough to fully safeguard its future. Additional measures should focus on keeping the natural habitat intact through regulating land use change in species-rich areas [61], reducing the impact at currently managed areas through adoption of biodiversity-friendly forestry/agriculture practices [15] or restoration efforts [62], and further controlling the underlying drivers such as human consumption to reduce land demand [63,64].

We identified hotspots of biodiversity loss under current and alternative future scenarios and note that these hotspots of future biodiversity loss differ depending upon the scenario, taxon, and metric considered (Table 3; Figure 2; Tables S4 and S5). This lends support to calls to carry out multi-indicator analyses in order to get a more comprehensive picture of biodiversity change [65].

Overall, the quantitative information we present here should inform the production and implementation of conservation actions. Combining multiple threats (i.e., climate, habitat loss, direct human pressure, and fragmentation) with the coupled RCP-SSP scenarios should allow more accurate predictions of biodiversity change. Given that we can allocate these predictions to particular land uses at the country level, incorporating country-level funding and development information (e.g., Waldron et al. [66]) is a logical next step. Such country-level projections should allow better allocation of conservation resources, necessary to move us towards the United Nations (UN) *Aichi* Target 13 (preserving genetic diversity) and UN SDG 15 (conserving terrestrial biodiversity).

Supplementary Materials: The following are available online at http://www.mdpi.com/2071-1050/10/8/2764/s1: Table S1: Model parameterization details. Data sources of countryside species–area relationship (SAR) model parameters. Table S2: Model validation results. Goodness-of-fit metrics calculated by comparing model predicted extinctions per ecoregion (Equation (1), main text) with number of species documented as threatened with extinction by IUCN Red List in each ecoregion. Table S3: Past, present, and future rates of projected biodiversity loss. Taxon-specific rates of biodiversity loss in endemic species extinctions per million species years (Equation (2)) and PD loss per million phylogenetic years (Equation (5)). Mean values along with 95% confidence interval are presented. Table S4: Additional biodiversity loss projected in each terrestrial ecoregion under six future scenarios. Additional number of species and phylogenetic diversity (in millions of years) committed to extinction in each ecoregion (804 total) due to land use change projected between 2015–2050 and 2015–2100 under five RCP-SSP scenarios. Table S5: Additional biodiversity loss projected in each country under six future scenarios. Additional number of species and phylogenetic diversity (in millions of years) committed to extinction in each country (176 total) due to land use change projected between 2015–2050 and 2015–2100 under five RCP-SSP scenarios. Table S6: Land use drivers of endemic species extinctions per country in 2050. Number of endemic species committed to extinction per country due to individual land use type under different RCP-SSP combination scenarios. Total projected extinctions were allocated to individual land use types through the allocation factor (Equation (6), main text). Table S7: Land use drivers of endemic species extinctions per country in 2100. Number of endemic species committed to extinction per country due to individual land use type under different RCP-SSP combination scenarios. Total projected extinctions were allocated to individual land use types through the allocation factor (Equation (6), main text). Figure S1: Scatter plots of projected species loss and PD loss of (a). mammals, (b). birds and (c). amphibians for the year 2015.

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