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Projecting impacts of climate change on global terrestrial ecoregions

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ABSTRACT

Terrestrial ecoregions, including critical ecoregions (CEs), vulnerable ecoregions (VEs), and intact ecoregions (IEs) have been used by the World Wildlife Fund (WWF) to classify global biodiversity and are being affected by climate change, which was considered as one of the main threats to biodiversity conservation. However, the impacts of future climate change in shifted means and extremes of temperature, precipitation, and cloud cover under the representative concentration pathways (RCP 2.6, 4.5, and 8.5) on the characteristics of these ecoregions have yet to be fully understood. The present study was designed using a dynamic global vegetation model and both current and future climate scenarios, to investigate the impacts of shifted means and extremes of temperature, precipitation, and cloud cover on five ecological indicators including net primary productivity (NPP), carbon storage, runoff, wildfire risk, and habitat transformation at the ecoregional scale. The analysis was performed for the terrestrial ecoregions as a whole, as well as for specific subsets of CEs, VEs, and IEs. The results showed that future climate scenarios (whether RCP 2.6, 4.5, or 8.5) were estimated to increase the mean NPP, runoff, wildfire risk, and habitat transformation for all ecoregion types, when comparing values for 2071–2100 to the baseline (1971–2000) period. In contrast, the mean carbon storage in the TEWs, VEs, and CEs was estimated to decrease from the baseline to the values under RCP 2.6 and RCP 4.5 and then increase to their largest values under RCP 8.5. The mean carbon storage in the IEs under RCP 8.5 was estimated to remain lower than the baseline period values. Climate change in shifted means and extremes of temperature, precipitation, and cloud cover are generally significant drivers of the variances of NPP, carbon storage, runoff, wildfire risk, and habitat transformation under RCP 2.6, RCP 4.5, and RCP 8.5. The dynamics of the climate change metrics and the five ecological indicators have significant implications for biodiversity conservation in changing climates.

1. Introduction

Climatic variables related to temperature, precipitation, and cloud cover, etc are changing, and according to the Intergovernmental Panel on Climate Change (IPCC, 2013), climate change includes: 1) unprecedented levels of atmosphere and ocean warming, diminishing snow and ice cover, rising sea levels and increasing concentrations of greenhouse gases. Global warming is universally considered one of the prominent features of climate change, whereas human activities are thought of as the dominant cause of the observed global warming since the mid-20th century. The global averaged combined land and ocean surface temperature has increased by ~0.85 °C from 1880 to 2012 and is projected to increase by more than 1.5 °C by the end of the 21st century compared with the value during the period from 1850 to 1900; 2) some more frequent and severe extreme climatic events. Global warming has likely contributed to the increased frequency of heat waves in many parts of Europe, Asia, and Australia and to the increased frequency and intensity of droughts in the Mediterranean and West Africa; 3) anthropogenic activities induced global-scale changes in the water cycle. In response to the warming over the 21st century, the contrast in precipitation between wet and dry regions and between wet and dry seasons will increase; and 4) human activities induced changes in radiation forcing and regional cloud cover.

The direct and indirect effects of global warming on both terrestrial and marine ecosystems have been documented (Diffenbaugh and Field, 2013; Hoegh-Guldberg and Bruno, 2010). The degradation of natural habitat by climate change is a major threat to biodiversity (Lewis, 2006; Pacifici et al., 2015). Both animals' and plants' responses to global warming have been widely discussed (Pacifici et al., 2015), and climate change is projected to be one of the most important drivers of biological

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Table 1
Global biodiversity conservation prioritization schemes.

Conservation schemes	Priorities	References
Biodiversity hotspots	Endemic species	(Myers et al., 2000)
Crisis ecoregions	Biomes and ecoregions at risk	(Hoekstra et al., 2005)
Endemic Bird Areas	Endemic birds	(Stattersfield et al., 1998)
Centers of Plant Diversity	Plants	(WWF, 1994)
Megadiverse countries	Endemic species	(Stattersfield et al., 1998)
Global 200 Ecoregions	Exceptional ecoregions	(Olson and Dinerstein, 2002)
Terrestrial ecoregions of the world	Exceptional ecoregions	(Olson et al., 2001)
High-biodiversity Wilderness Areas	High-biodiversity wild areas	(Olson and Dinerstein, 1998)
Frontier forests	Natural forest ecosystems	(Bryant et al., 1997)
Last of the Wild	Wild areas	(Sanderson et al., 2002)
World's Protected Areas	Natural environment and biodiversity	(IUCN, 2014-2015)

extinction during the 21st century (Lewis, 2006; Pereira et al., 2010; Sala et al., 2000; Thomas et al., 2004). It is also estimated that, by the end of the 21st century, plant communities on 49% of the Earth's land surface will undergo climate-driven changes and 37% of the world's terrestrial ecosystems will experience biome-scale changes (Bergengren et al., 2011). Furthermore, increasing evidence indicates that climate change and habitat loss and fragmentation interact to exert negative effects on biodiversity (Mantyka-pringle et al., 2012). For example, climate change was estimated to act in concert with land use and land cover change to severely affect biodiversity in developing countries (Visconti et al., 2011). As temperature increases, reptiles are most likely to be negatively affected by habitat loss/fragmentation (Mantyka-pringle et al., 2012).

Global patterns in the distribution and threats to biodiversity are very non-uniform due to unbalanced resource distribution and variable stresses (Gaston, 2000). Therefore, in order to minimize losses of global biodiversity and to effectively allocate limited resources for biodiversity conservation, biodiversity conservation organizations have developed at least 11 global biodiversity conservation prioritization schemes (Table 1).

Most of these schemes assign high importance to region irreplaceability and vulnerability and promote both reactive (prioritizing high vulnerability) and proactive (prioritizing low vulnerability) measures to allocate conservation funding more effectively and flexibly over multiple geographic areas (Brooks et al., 2006). Ecoregions represent one of the most established global biodiversity conservation schemes, and special emphasis is placed on identifying unique biodiversity and its biogeographic distributions (Olson et al., 2001; Olson and Dinerstein, 2002). An ecoregion base map has been adopted by the World Wildlife Fund (WWF), the World Bank, the World Resources Institute, the Nature Conservancy, and several other organizations in order to allocate funding to global biodiversity conservation (Olson et al., 2001). For the terrestrial ecoregions of the world, the most prominent threat to conservation is habitat loss, followed by habitat fragmentation, degree of degradation, and degree of protection (Olson and Dinerstein, 2002). The WWF has divided ecoregions into three broad categories: critical or endangered ecoregions (CEs), which are at extremely high risk of extinction in the wild; vulnerable ecoregions (VEs), which are at high risk of endangerment in the wild; and intact ecoregions (IEs), which are relatively stable.

The changing climate raises concern about the viability of and mechanisms by which species in different terrestrial ecoregions will be able to adapt and persist in future climate conditions. Therefore, it is now necessary to integrate climate change scenarios into long-term conservation strategies, in order to comprehensively address multiple threats to biodiversity. Because vegetation is an important indicator of biodiversity for the vast majority of species, including plants and animals (Olson et al., 2001), quantifying the magnitude and patterns of vegetation and habitat changes, as well as the associated ecological dynamics, has become an important aspect in the science and practice of global biodiversity conservation.

In the present study, we used terrestrial ecoregions as the analysis units, and current and future temperature, precipitation, and cloud cover data as inputs to a dynamic global vegetation model to accomplish the following two objectives: (1) to compare changes in vegetation type and five associated ecological indicators (net primary productivity (NPP), carbon storage, runoff, wildfire risk (carbon loss by fire), and habitat transformation) between the 1971–2000 baseline period and the 2071–2100 projection period; (2) to identify the climate drivers of the five ecological indicators in terms of shifted means and extremes of temperature, precipitation, and cloud cover. This study may provide meaningful understanding of the dynamics of climate change metrics and ecological dynamics that have vital implications for biodiversity conservation at the ecoregion scale and under changing climates.

2. Materials and methods

2.1. Lund-Potsdam-Jena dynamic global vegetation model and simulated ecological indicators

The Lund-Potsdam-Jena dynamic global vegetation model (LPJ-DGVM) (Sitch et al., 2003) is a process-based model that represents large-scale terrestrial vegetation dynamics, as well as carbon and water cycles. The main biophysical processes include photosynthesis, evapotranspiration, resource competition, tissue turnover, population dynamics, soil organic matter and litter dynamics, and fire interference mechanisms, as well as their interactions. Plant functional types (PFTs) in the LPJ-DGVM are confirmed according to the diversities in their physiological, morphological, phonological, bioclimatic, and fire-response features. The LPJ-DGVM is driven by monthly mean temperature, total precipitation, cloud cover, annual atmospheric CO_2 concentration, and soil texture. We used temperature, precipitation, and cloud cover datasets as inputs into version 3.1 of the LPJ-DGVM, in order to calculate vegetation composition, NPP, carbon storage, runoff, and wildfire risk. The nine PFTs included tropical broad-leaved evergreen trees, tropical broad-leaved deciduous trees, temperate needle-leaved evergreen trees, temperate broad-leaved evergreen trees, temperate broad-leaved deciduous trees, boreal needle-leaved evergreen trees, boreal broad-leaved deciduous trees, C3 perennial grasses, and C4 perennial grasses. Areas of desert and ice, where the vegetation cover was below 10%, were excluded from the analysis, and current urban and agricultural areas were masked based on the Global Land Cover 2000 dataset (Bartholome and Belward, 2005). Each PFT was assigned specific parameters, including phenology, carbon pathway, and leaf type (e.g., C:N mass ratios for leaf, sapwood, and roots). Carbon storage was estimated in terms of the net fluxes of carbon exchange between the atmosphere and land biosphere and was calculated as: carbon storage = NPP − (heterotrophic respiration + carbon loss by fire), where positive carbon storage values indicate that the land is a carbon sink, and negative carbon storage values indicate that land is a carbon source.

The LPJ-DGVM was run from 1901 to 2100 (with a 1000-year spinup) on a regular latitude-longitude grid (0.5° × 0.5°). Monthly mean temperature (1901–2005), total precipitation (1901–2005), and cloud cover (1901–2005) data were collected from the CRU TS 3.1 dataset (Harris et al., 2014), whereas soil texture data was collected from the NASA ISLSCP GDSLAM Hydrology-Soils dataset (Webb et al., 1993). Projected annual atmospheric mean CO_2 concentration (1901–2100), monthly mean temperature (2006–2100), total precipitation (2006–2100), and cloud cover (2006–2100) were collected from the Coupled Model Intercomparison Project Phase 5 (CMIP5). We selected the three representative concentration pathways (RCP 2.6, 4.5, and 8.5) (van Vuuren et al., 2011) as projected climate scenarios during 2071–2100. The RCP 2.6 scenario assumes that global annual greenhouse gas (GHG) emissions will peak around 2020 and then substantially decline thereafter. The RCP 4.5 scenario assumes that GHG emissions will peak around 2040 and then decline, and the RCP 8.5 scenario assumes continued anthropogenic GHG emissions after 2100. As a result, global surface temperature is expected to increase by 0.3 °C to 1.7 °C in the RCP 2.6 scenario, by 1.1 °C to 2.6 °C in the RCP 4.5 scenario, and by 2.6 °C to 4.8 °C in the RCP 8.5 scenario for 2081–2100 relative to 1986–2005 (IPCC, 2013).

Climate models vary in their suitability to project specific climate variables in different regions. Therefore, to prevent the uncertainty resulting from the use of a single climate model, we used the ensemble mean values of the mean monthly temperature, total monthly precipitation, and total monthly cloud cover under the RCP 2.6, RCP 4.5, and RCP 8.5, which were projected by the 14 atmosphere-ocean general circulation models (GCMs) from the CMIP5 (Supplementary Table 1) to run the LPJ-DGVM. Mean standard deviation (MSD, see the following equation (1)) was used to quantify uncertainty in the temperature, precipitation, and cloud cover values projected by the 14 GCMs, with higher MSDs indicating greater variation than lower MSDs (Supplementary Fig. 1).

$$\mathrm{MSD} = \frac{1}{n}\sqrt{\frac{1}{m}\sum_{i=1}^{m}(x_i - \mu)^2} \tag{1}$$

where n is the number of the climate models (n = 14), m is the size of a certain climate variable (temperature, precipitation, or cloud cover) sample (m = 30, corresponding to the period of 2071–2100), x_i are the values of a certain climate viable from 2071 to 2100, and μ is the mean value of a certain climate viable from 2071 to 2100.

PTFs for the 1971–2000 period and projected for the 2071–2100 period under RCP 2.6, RCP4.5, and RCP8.5 are shown in Fig. 2.

2.2. Basic spatial unit

Terrestrial ecoregions were used as basic spatial unit because they are widely accepted as a useful priority scheme for the conservation of global biodiversity (Olson and Dinerstein, 2002). Ecoregions are defined as "relatively large units of land containing a distinct assemblage of natural communities and species and provide a framework for comparisons among units and the identification of representative habitats and species assemblages" (Olson and Dinerstein, 2002).

The terrestrial ecoregions of the world is divided into 867 ecoregions (Olson et al., 2001). In the present study, the ecoregions with areas less than 5 km^2 were excluded from analysis because they were too small to correspond with the map units defined under the simulation's spatial resolution (0.5° × 0.5°). Therefore, the study analyzed 852 ecoregions (Fig. 1), including 423 CEs, 221 VEs, and 208 IEs. Greenland and Antarctica were not included in this study.

Shapefile polygons of the TEWs, CEs, VEs, and IEs were overlaid with simulated grid ecological indicators, in order to calculate mean NPP, carbon storage, runoff, wildfire risk, and habitat transformation, to detect changes in these parameters between the baseline (1971–2000) and future (2071–2100) periods, and to identify climatic drivers of the parameters. If the area of a specific ecoregion was smaller than that of an individual grid cell (~2500 km^2) but larger than 5 km^2, the ecological indicator values of the ecoregion were calculated as equivalent to those of the grid cell (because the inside of each grid is homologous). Habitat transformation was defined as the whole PFT percentage (Fig. 2) changing within an ecoregion unit (Fig. 1) between the baseline (1971–2000) and future (2071–2100) periods.

2.3. Climate drivers of ecological indicators

Climate change is characterized by shifts in climatic means and extreme events (IPCC, 2013). Mean shifts in temperature, precipitation, and cloud cover were defined as differences in the grid-based means of the baseline (1971–2000) and future (2071–2100) periods (Supplementary Fig. 2). Changes in the frequency and intensity of extreme temperature, precipitation, and cloud cover events were defined as differences in the frequency and intensity of extreme monthly means (Supplementary Figs. 3–4), which were defined as those that differed from the corresponding means (M) of the baseline (1971–2000) and future (2071–2100) periods by more than two standard deviations (σ). The distance (D) was also calculated for monthly mean temperature, precipitation, and cloud cover by normalizing the difference between the means of the baseline (1971–2000) and future (2071–2100) periods for each 0.5° × 0.5° grid cell, as follows:

$$\mathrm{D} = (\mathrm{M}_{2071-2100} - \mathrm{M}_{1971-2000})/\sigma_{1971-2000}, \tag{2}$$

The 2σ criterion is suitable for identifying climate extremes (Beaumont et al., 2011; Luterbacher et al., 2004). Changes in both the mean frequency and mean intensity of extreme events were calculated.

For an individual ecoregional polygon, mean differences between the baseline (1971–2000) and future (2071–2100) periods were calculated for each of the nine climate change variables and five ecological indicators. The nine climate change variables were divided into three categories: shifted means including mean temperature (T_m), mean precipitation (P_m), and mean cloud cover (C_m); the frequencies of climatic extremes including extreme temperature (T_f), extreme precipitation (Pf), and extreme cloud cover (C_f), and the intensities of climatic extremes in terms of extreme temperature (T_i), extreme precipitation (P_i), and extreme cloud cover (C_i). Analysis of variance (ANOVA) was used to examine the effects of changes in temperature, precipitation, cloud cover, and their interactions on NPP, carbon storage, runoff, wildfire risk, and habitat transformation at the global ecoregional scale, using a significance level of $p < 0.05$ (Fig. 3).

3. Results

3.1. Changes in ecological indicators

The 852 TEWs covered a total area of 1.18 × 10^8 km^2, accounting for 95.6% of the WWF's global ecoregions, and the VEs, CEs, and IEs accounted for 34.78%, 39.44%, and 21.35% of the WWF's global ecoregions, respectively (Fig. 4a). From the benchmark to RCP 8.5, both NPP and runoff increased for all four ecoregion categories (Fig. 4b, d), and under RCP 2.6 and RCP 4.5, the carbon storage of all four ecoregion categories was second only to that observed during the baseline period and then increased to its largest values under RCP 8.5 for TEWs, VEs, and CEs (Fig. 4c). From the baseline to RCP 8.5, the wildfire risk of all four ecoregion categories increased (Fig. 4e). Therefore, future climate change will likely result in notable habitat transformations (Fig. 4f), since 40%, 42–48%, and > 50% of habitats are predicted to undergo transformation under RCP 2.6, RCP 4.5, and RCP 8.5, respectively.

Generally, the NPP of most ecoregions is predicted to increase with climate change, independently of the type of ecoregion or emission scenario considered (Fig. 5a–c). However, the NPP of certain tropical evergreen forests, tropical rainforests, alpine shrub and meadows, and dry forests is predicted to suffer losses. Global warming is predicted to increase heterotrophic respiration, thereby reducing the carbon storage

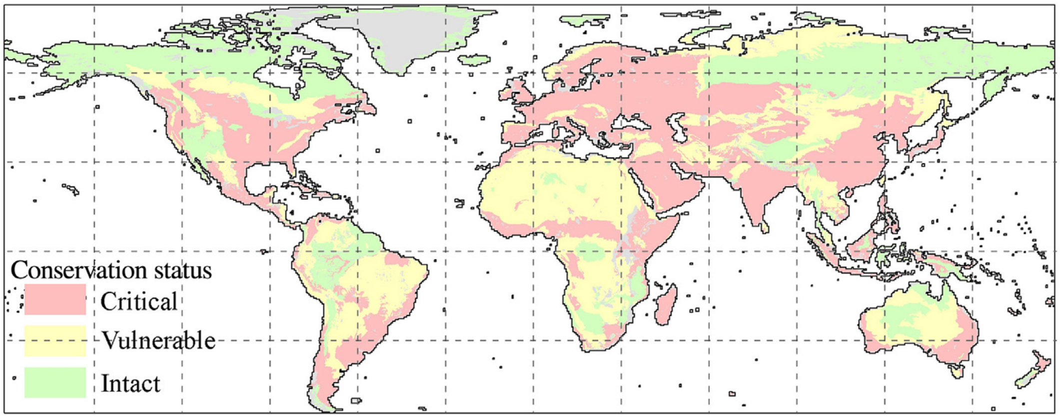

Fig. 1. Terrestrial ecoregions of the world.

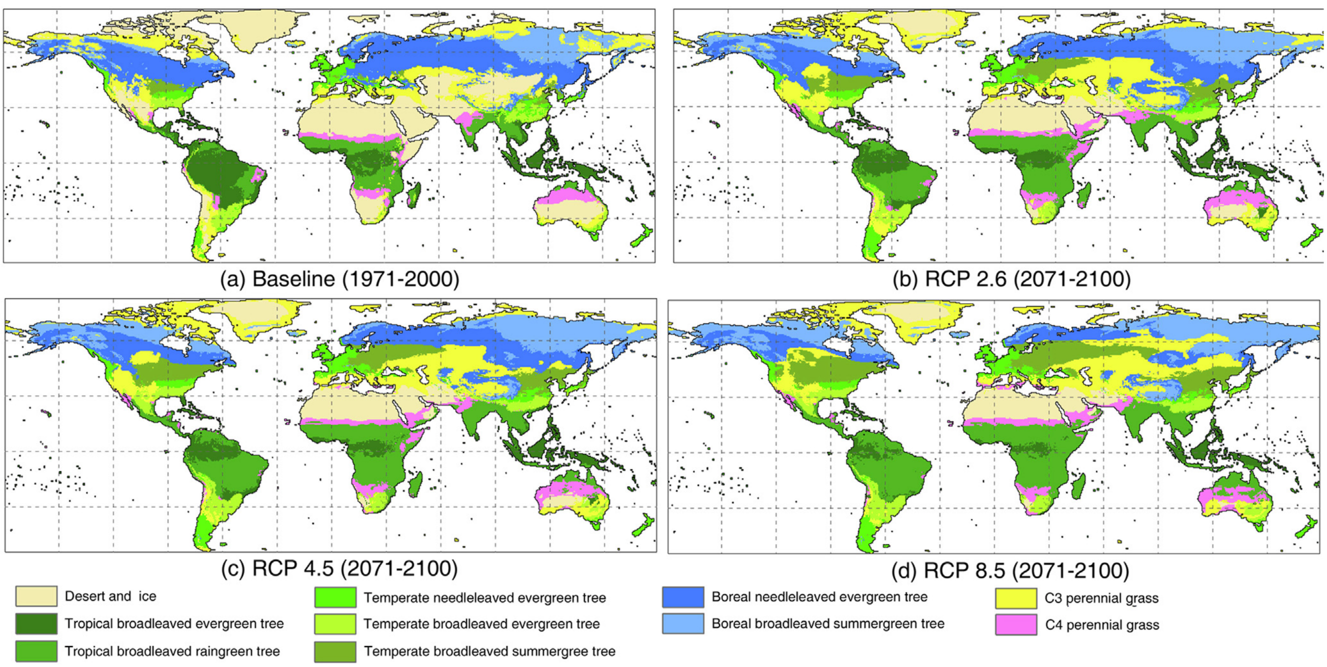

Fig. 2. PFTs for (a) the 1971–2000 baseline period and PFTs for climate scenarios of (b) RCP 2.6, (c) RCP 4.5, and (d) RCP 8.5 during the 2071–2100 period.

of more than half the ecoregions under RCP 2.6 and RCP 4.5, although the situation is predicted to be slightly ameliorated by the fertilization effect under RCP 8.5 (Supplementary Table 2 and Fig. 5d-f). Under RCP 2.6 and RCP 4.5 (Fig. 5d-e), carbon storage in some tropical evergreen forests and rainforests in South America, Central Africa, Madagascar, East Asia, New Guinea, and north Australia will decrease, and the carbon storage of boreal needle-leaved and temperate broad-leaved forests in North America, temperate forests in east China, grasslands, and high-altitude boreal forests will also decline. Under RCP 8.5 (Fig. 5f), carbon storage is predicted to be reduced in certain temperate broad-leaved forests and grasslands in North America, and the boreal broad-leaved forests, temperate broad-leaved forests, and certain grasslands in east China and Russia will experience significant carbon sink losses. Furthermore, most ecoregions are predicted to experience increased runoff, regardless of RCP (Fig. 5g–i); however, certain ecoregions in South America, Madagascar, the Australian Outback, Mediterranean areas, and east China are predicted to become drier. Under the three RCP scenarios, most CEs, VEs, and IEs are predicted to face a higher wildfire risk, especially ecoregions with tropical forests (Fig. 5j–l). Habitat-type transformation is predicted widely across CEs, VEs, and IEs (Fig. 5m–o). Habitat transformation will occur extensively, especially in some South American ecoregions where tropical broad-leaved evergreen forests will be replaced by tropical broad-leaved deciduous forests and in the southeastern United States where certain grasslands will be replaced by temperate broad-leaved evergreen forests (Fig. 2, Fig. 5m–o). In addition, temperate deciduous forests greatly expanded into the central ecoregions of the United States, and C3 grasslands expanded into the ecoregions of northern Canada. C3 grasslands in South Africa were replaced by C4 grasslands and temperate needle-leaved evergreen forests (Fig. 2, Fig. 5m–o). In Eurasia, temperate broad-leaved deciduous forests will expand largely to replace certain boreal needle-leaved evergreen forests and C3 grasslands, and both boreal broad-leaved deciduous forests and C3 grasslands will expand north towards high-latitude ecoregions. In Australia, C4 grasslands and forests will expand into the desert ecoregions (Fig. 2, Fig. 5m–o).

The NPP, carbon storage, and runoff of many more VEs, CEs, and IEs will increase (Figs. 5 and 6). As indicated in Fig. 6, the percentage of ecoregions with wildfire risk is the highest for IEs, followed by VEs and CEs. More than > 80% of ecoregions will experience increased habitat transformation, regardless of RCP. Furthermore, more than 40% of the CEs, VEs, and IEs will experience habitat transformation that exceeds

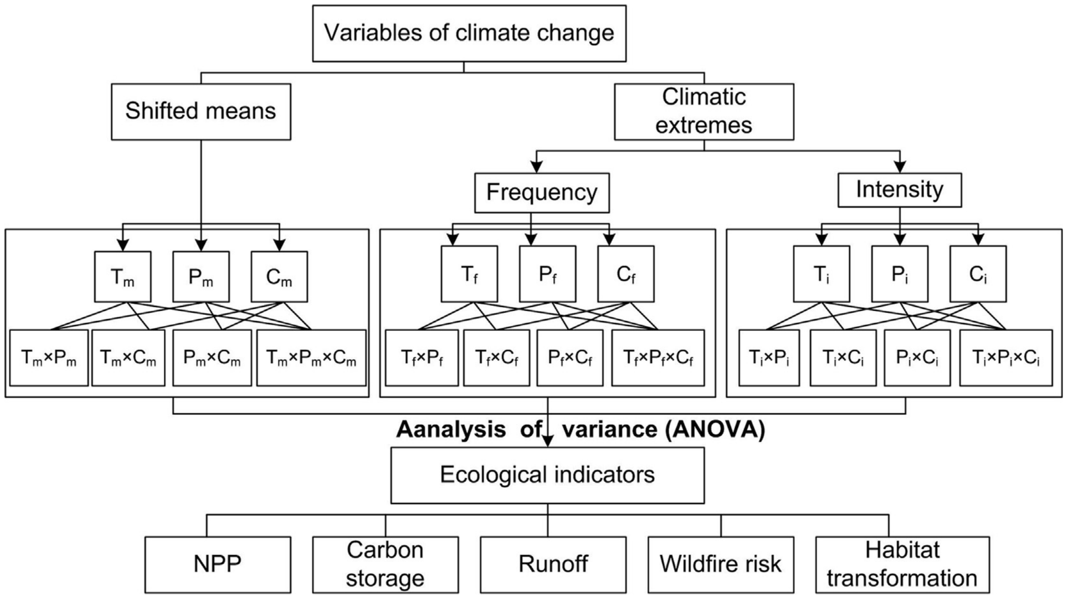

Fig. 3. Flowchart of analysis of variance (ANOVA) for the impacts of climate change variables on ecological indicators. Climate change is represented as shifted means and climatic extremes. Shifted means include mean temperature (T_m), mean precipitation (P_m), and mean cloud cover (C_m). Climatic extremes include the frequencies of extreme temperature (T_f), extreme precipitation (Pf), and extreme cloud cover (C_f) and the intensities of extreme temperature (T_i), extreme precipitation (P_i), and extreme cloud cover (C_i). ×: interaction of climate change variables.

almost 50% under the three climate scenarios. Complete habitat transformation (100%) is predicted to occur in 31, 37, and 64 CEs; in 25, 26, and 38 VEs; in 20, 26, and 39 IEs under RCP 2.6, RCP 4.5, and RCP 8.5.

3.2. Climatic drivers of ecological indicators

3.2.1. Impacts of changes in climatic means on ecological indicator variances

Changes in mean precipitation and cloud cover are predicted to have significant impacts on the NPP variance under the three RCPs, while mean temperature is predicted to have a significant impact under RCP 2.6 and RCP 8.5 (Supplementary Table 2). The interactions between mean temperature–cloud cover, precipitation–cloud cover, and temperature–precipitation–cloud cover will significantly influence NPP variances under the three RCPs, while the temperature– precipitation interaction only shows a notable impact on the NPP variance under RCP 2.6. Changes in mean temperature and precipitation are predicted to result in significant impacts on carbon storage variance under RCP 2.6 and RCP 4.5. Although both shifted mean temperature and precipitation are not predicted to notably affect carbon storage under RCP 8.5, the interaction of these two variables is predicted to have an effect on carbon storage. Changes in mean cloud cover and the interactions between mean temperature–precipitation and among mean temperature–precipitation–cloud cover are predicted to have significant impacts on carbon storage variance under the three RCPs. The interactions between mean temperature–cloud cover under RCP 4.5 and between mean precipitation–cloud cover under RCP 4.5 and RCP 8.5 are predicted to have significant impacts on carbon storage variance.

Except for the interaction between mean temperature–cloud cover under RCP 4.5, both the individual mean climatic variables and their interactions are predicted to have significant impacts on runoff variance under the three RCPs. Changes in mean temperature and precipitation and the interactions between them, as well as between mean precipitation–cloud cover are predicted to significantly impact on wildfire risk under the three RCPs. Changes in mean cloud cover under RCP 2.6 and the interactions between mean temperature–cloud cover and among mean temperature–precipitation–cloud cover under RCP 2.6 and RCP 4.5 will also significantly affect the variance of wildfire risk. Changes in mean temperature under the three RCPs and the interaction between precipitation–cloud cover under RCP 2.6 and RCP 8.5 are predicted to play key roles in inducing habitat transformation.

3.2.2. Effect of the intensities of climatic extremes on ecological indicators

NPP is predicted to be significantly affected by extreme temperature intensity only under RCP 2.6, by extreme precipitation intensity under RCP 2.6 and RCP 4.5, by extreme cloud cover intensity under RCP 2.6 and RCP 8.5, and by the interaction between extreme precipitation intensity and extreme cloud cover under RCP 2.6 and RCP 4.5 (Supplementary Table 3).

Meanwhile, carbon storage is predicted to be significantly affected by extreme temperature intensity, under RCP 2.6 and RCP 8.5, and by extreme precipitation intensity and extreme cloud cover intensity under RCP 2.6 and RCP 4.5, respectively. In addition, carbon storage is also predicted to be significantly affected by the interaction between extreme temperature intensity and extreme cloud cover intensity, regardless of RCP, by the interaction between extreme temperature intensity and extreme precipitation intensity under RCP 8.5, and by the three-way interaction among extreme temperature intensity, extreme precipitation intensity, and extreme cloud cover intensity under RCP 2.6 and RCP 4.5.

Significant effects were also predicted for runoff, wildfire risk, and habitat transformation. Runoff is predicted to be significantly affected by extreme temperature intensity and extreme cloud cover intensity under RCP 2.6 and RCP 8.5 and by extreme precipitation intensity and all interactions under all three RCPs. In contrast, wildfire risk is predicted to be significantly affected by extreme precipitation (i.e., drought) intensity and the interaction between extreme precipitation intensity and extreme cloud cover intensity under all three RCPs, as well as by extreme cloud cover intensity and the interaction between extreme temperature intensity and extreme cloud cover intensity under RCP 2.6 and by the three-way interaction among extreme temperature intensity, extreme precipitation intensity, and extreme cloud cover intensity under RCP 2.6 and RCP 4.5. For habitat transformation, extreme drought intensity was the most important significant factor under all three RCPs, followed by extreme cloud cover intensity, under RCP 2.6 and RCP 8.5, and the three-way interaction between extreme temperature intensity, extreme precipitation intensity, and extreme cloud

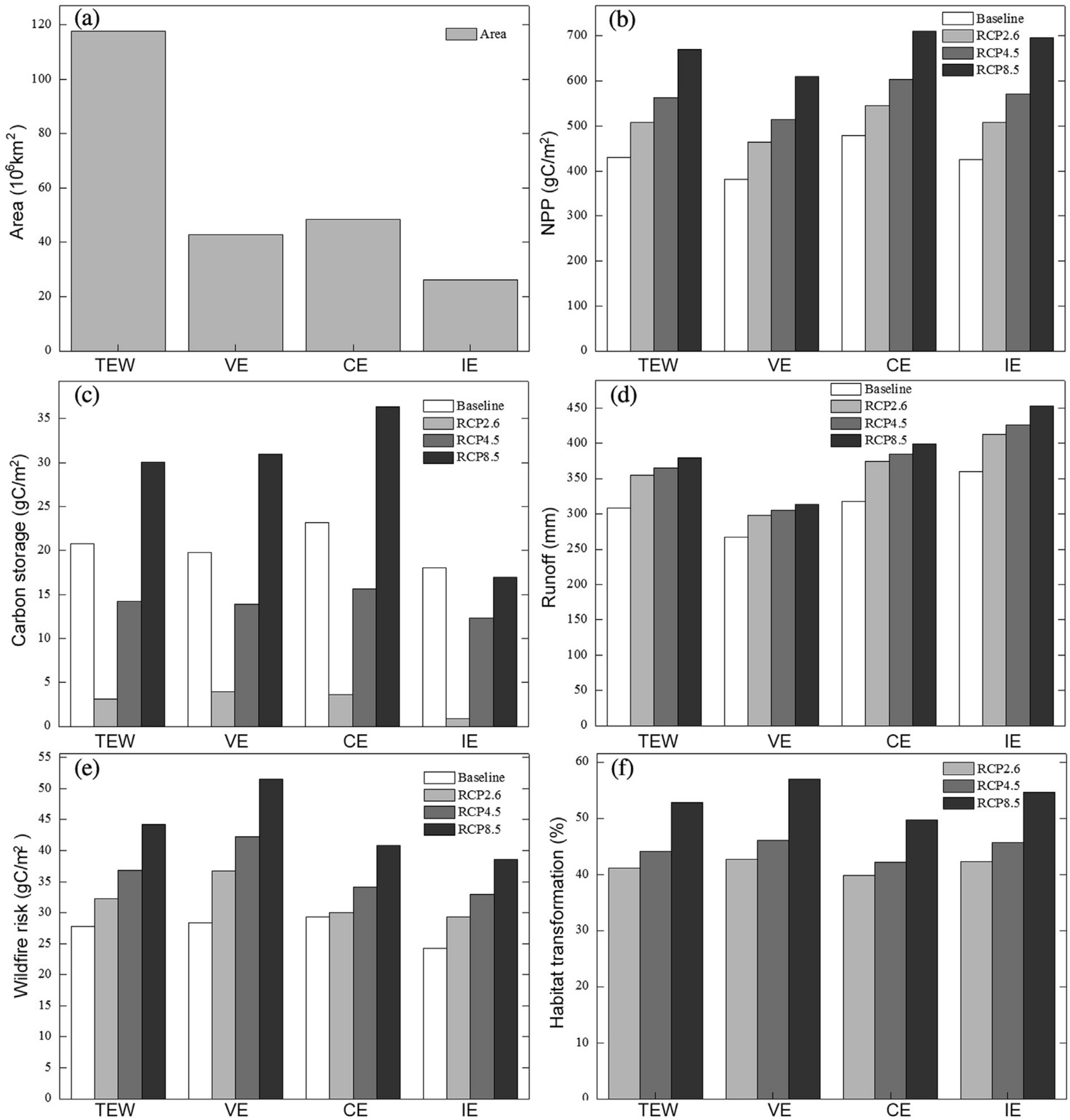

Fig. 4. (a) Total areas (b) mean NPP, (c) carbon storage, (d) runoff, (e) wildfire risk, and (f) habitat transformation values for terrestrial (TEWs, sample size = 852), critical (CEs, sample size = 423), vulnerable (VEs, sample size = 221), and intact (IEs, sample size = 208) ecoregions under the baseline (1971–2000) and future (2071–2100) climate scenarios.

cover intensity under RCP 8.5.

3.2.3. Effect of the frequencies of climatic extremes on the variances of ecological indicators

NPP is predicted to be significantly affected by extreme temperature frequency and extreme cloud cover frequency, under RCP 2.6, and by extreme precipitation frequency, the interaction between extreme temperature frequency and extreme precipitation frequency, and the interaction between extreme precipitation frequency and extreme cloud cover frequency under all three RCPs (Supplementary Table 4). The extreme temperature frequency and extreme cloud cover frequency are also predicted to affect NPP significantly under RCP 2.6 and RCP 4.5, as is the three-way interaction among extreme temperature frequency, extreme precipitation frequency, and extreme cloud cover frequency under RCP 4.5 and RCP 8.5.

Meanwhile, carbon storage is predicted to be affected by extreme cloud cover frequency, regardless of RCP, as well as by extreme precipitation frequency under RCP 2.6 and RCP 4.5, extreme temperature frequency under RCP 4.5, the interaction between extreme temperature frequency and extreme precipitation frequency under RCP 4.5, the interaction between extreme temperature frequency and extreme cloud cover frequency under RCP 2.6 and RCP 4.5, the interaction between extreme precipitation frequency and extreme cloud cover frequency under RCP 2.6, and the three-way interaction among extreme temperature frequency, extreme precipitation frequency, and extreme cloud cover frequency under RCP 2.6 and RCP 8.5.

Significant effects are also predicted for runoff, wildfire risk, and habitat transformation. Runoff is predicted to be significantly affected by extreme precipitation frequency, extreme cloud cover frequency, and all two-way interaction between extreme temperature frequency, extreme precipitation frequency, and extreme cloud cover frequency, regardless of RCP. Extreme temperature frequency is also predicted to

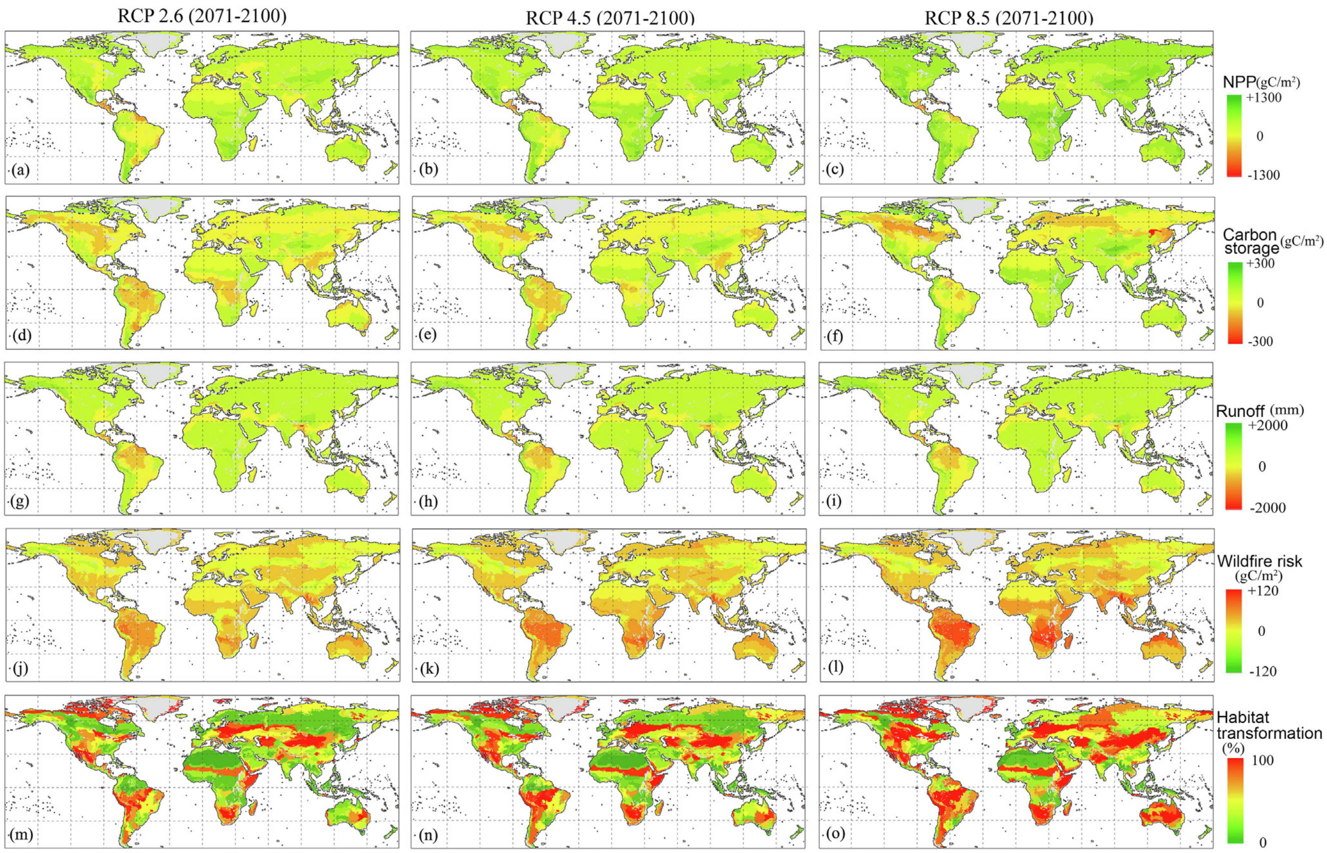

Fig. 5. Differences in the mean values of NPP (a, b, c), carbon storage (d, e, f), runoff (g, h, i), wildfire risk (j, k, l), and habitat transformation (m, n, o) of terrestrial ecoregions under RCP 2.6, RCP 4.5, and RCP 8.5 between the baseline period of 1971–2000 and the future period of 2071–2100.

have a significant effect on runoff under RCP 4.5 and RCP 8.5, as is the three-way interaction among extreme temperature frequency, extreme precipitation frequency, and extreme cloud cover frequency under RCP 2.6 and RCP 8.5. In contrast, wildfire risk is predicted to be significantly affected by extreme temperature frequency under RCP 2.6 and RCP 4.5, both extreme precipitation frequency and extreme cloud cover frequency under all three RCPs, the interaction between extreme temperature frequency and extreme cloud cover frequency under RCP 4.5, and the three-way interaction among extreme temperature frequency, extreme precipitation frequency, and extreme cloud cover frequency under RCP 2.6 and RCP 8.5. Habitat transformation is predicted to be significantly affected by extreme temperature frequency under RCP 4.5, extreme precipitation frequency under RCP 4.5 and RCP 8.5, and the three-way interaction among extreme temperature frequency, extreme precipitation frequency, and extreme cloud cover frequency under RCP 8.5.

4. Discussion

Climate change in terms of global warming is one of the most important forces driving ongoing biological extinction; it continues to affect biodiversity at local, regional, and global scales (Garcia et al., 2014; Pacifici et al., 2015; Rybicki and Hanski, 2013). Climate change can affect biodiversity both directly, by impacting species' behaviors and life histories, and indirectly, by altering species' habitats in terms of habitat loss and fragmentation (Mantyka-pringle et al., 2012). Climate change and habitat degradation are currently the two most important threats to global biodiversity, and their combined effects may greatly magnify their negative impacts. Understanding the combined effects of climate change and habitat-associated threats has critical implications for policy makers to update and improve current ecoregional biodiversity conservation measures. To date, little is known about such combined effects, mainly because of the underlying complexity of the two processes and differences in their individual effects.

In the present study, we quantified climate change in terms of shifted means and extremes of temperature, precipitation, and cloud cover between the 1971–2000 period and the 2071–2100 period as well as changes in the magnitudes and directions of five ecological indicators at the ecoregion scale and under multiple climate change scenarios. Our simulation indicated that global warming is universal under all three RCPs, especially in the Northern Hemisphere and under RCP 8.5; in some places, the temperature rise exceeded 6 °C (Supplementary Fig. 2). At the ecoregional scale, IE experienced the highest temperature increases, followed by CE and VE under all three RCPs. When global warming exceeds 3 °C, biological extinction risk increases by 8.5% (Urban, 2015). Although there is little direct cause-effect evidence between local extinction and high temperature, many studies indicated that species interactions, especially decreases in food availability with changing climate is an important cause of local extinction (Cahill et al., 2013). Therefore, with global warming, in addition to considering interspecific relationships, species with limited tolerances to high temperatures such as amphibians in the Northern Hemisphere and in IEs should be considered in future conservation measures. Our results showed that both frequency and intensity of the climatic extremes of temperature, precipitation (drought), and cloud cover increased during the 2071–2100 period compared with the 1971–2000 period (Supplementary Tables 6 and 7). Empirical studies have shown that warming and increased precipitation can promote plant growth and ecosystem carbon storage and that decreased precipitation has adverse impacts (Wu et al., 2011). When drought accompanies heat waves, the negative effects of heat stress can be amplified to decrease plant growth and even lead to plant mortality

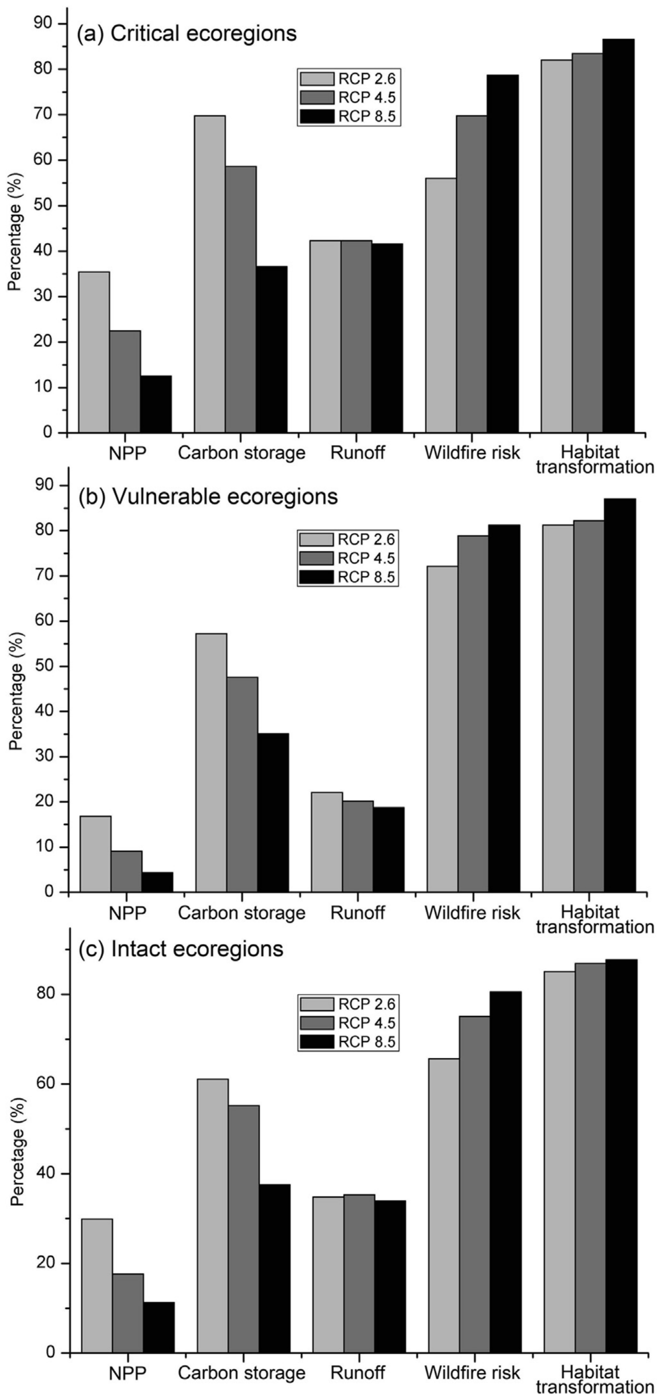

Fig. 6. Percentage (%) of each category of (a) critical ecoregions, (b) vulnerable ecoregions, and (c) intact ecoregions between baseline (1971–2000) and future (2071–2100) climate scenarios that have decreases in net primary productivity (NPP), carbon storage, and runoff and increases in wildfire risk and habitat transformation.

(Teskey et al., 2015). Our simulation indicated that some tropical ecoregions in South America, Central Africa, and Southeast Asia are sensitive hotspots with decreases in ecosystem carbon storage (Fig. 5), where the intensity of precipitation decreases is relatively larger (Supplementary Fig. 4). It is important to note that certain ecoregions in South America are vital to conserving global biodiversity. The Neotropics, for example, contain the largest remaining wilderness areas and harbor the highest species richness in the world (Loyola et al., 2009). Indeed, the Atlantic forest harbors 19,355 species, 40% of which are endemic to Brazil, and the Cerrado (i.e., the Brazilian savannah) contains the richest savanna flora in the world, with 12,669 species, of which 4215 are endemic (Forzza et al., 2012). However, the findings of the present study indicated that these regions incurred greater pressures from climate change. The temperature increases in the Southern Hemisphere reduce water availability and nonlinearly amplify ecological risk, representing a great threat to biodiversity and NPP (Zhao and Running, 2010). Comparatively, warming in the Northern Hemisphere would release the constraint of low temperature on vegetation growth and increase vegetation productivity, while a higher heterotrophic respiration rate simultaneously weakens the ability of the ecosystem to store carbon (Fig. 5). Some generalist species may benefit from the expansion of ranges due to warming, whereas some limited-ranges species would be potentially harmed by warming in the Northern Hemisphere. To what extent species will benefit or suffer as a result of Northern Hemisphere warming has not been previously well studied. Additionally, our simulation showed that mean cloud cover in all ecoregion categories (CE, IE, and VE) decreased (Supplementary Table 5), and both the frequency and intensity of extreme cloud cover increased (Supplementary Tables 6 and 7). Reduced cloud cover may increase incident solar radiation, which, along with other stressors, could affect amphibian persistence by increasing mortality, developmental abnormalities, disease susceptibility, and behavioral changes and by reducing growth *via* elevated ultraviolet-B levels (UV-B: 280–315 nm) (D'Amen and Bombi, 2009). In addition, ultraviolet-A radiation (UV-A: 315–400 nm) has been reported to inhibit and stimulate the biomass accumulation and morphology of common plants (Verdaguer et al., 2017). However, little is known about how variations in solar radiation would affect species composition and the interaction of organisms between trophic levels within natural ecosystems for changing climate (Haeder et al., 2011).

Our simulations indicated that further habitat degradation in changing climate conditions would be universal across ecoregions and that shifts in the means and extremes of temperature, precipitation, and cloud cover were significant drivers. Global warming can amplify the amplitude of temperature, precipitation, cloud cover, and other climate variables, and on the other hand, it can act in concert with habitat degradation to affect biodiversity. A meta-analysis of 1319 studies across the globe indicated that among the influential factors (maximum temperature, minimum precipitation, mean precipitation change, mean temperature change, and habitat availability) on species density and diversity, the most important factor contributing to the negative effects of habitat loss and fragmentation was the current maximum temperature, closely followed by the mean precipitation change over the last 100 years (Mantyka-Pringle et al., 2012). In other words, the negative effects of habitat degradation are generally greater in areas with higher temperatures but ameliorated by increases in mean precipitation. As the intensity of the climate change scenarios increased (i.e., from RCP 2.6 to RCP 8.5), habitat transformation and both the extreme and mean temperature parameters increased in all three ecoregion categories (i.e., CEs, VEs, and IEs; Fig. 4, Supplementary Tables 5–7). Even though in most cases, the mean precipitation increased in all three ecoregion categories (Supplementary Table 5), the magnitudes of precipitation increase were less than the magnitudes of temperature rise. Therefore, the combined negative effects of habitat degradation and climate change on global biodiversity are also expected to worsen under intensifying climate change scenarios. Furthermore, the extreme and mean temperature values were higher in the CEs and IEs, respectively, which indicate that the risk of biodiversity loss was relatively greater in these ecoregions, with the greatest risks of biodiversity loss in the ecoregions with the greatest amplitudes of temperature elevation and precipitation reduction. The combined negative effects of climate change and habitat degradation are especially significant for limited-range species. Conservation efforts should prioritize species vulnerable to temperature increases, especially in habitats such as wetlands, savannas, grasslands, and rainforests, where the combined effects of habitat and climate change are expected to be particularly impactful (Mantyka-pringle et al., 2012).

In the present study, we also simulated the dynamics of NPP, carbon storage, runoff, wildfire, and habitat transformation. As an overall measure of an ecosystem's ability to produce biomass, NPP is also an indicator of energy availability and can be used to predict species abundance and occurrence (Wright, 1983). At a regional scale, NPP is a good indicator of plant species richness, and elevated CO_2 concentrations were predicted to improve diversity capacity by increasing NPP (Woodward and Kelly, 2008). Carbon storage indicates the terrestrial biosphere's ability to mitigate anthropogenic CO_2 release and is critical to reversing global warming. It is increasingly important to improve our understanding of the relationship between biodiversity and carbon sinks and how to promote a win-win scenario between them. However, the relationship between biodiversity and carbon sequestration at the global scale remains poorly understood (Midgley et al., 2010). For example, even though a strong positive relationship has been reported for global carbon stocks and species richness, the synergies between the two are highly unevenly distributed (Strassburg et al., 2010). Indeed, forest ecosystems are critical for conserving carbon stocks and biodiversity in the tropics, whereas underground carbon stocks are of greater importance in species-poor polar and subpolar latitudes (Midgley et al., 2010). Global warming may result in amplifying the hydrological cycle and thus lead to more extreme rainfall (Knapp et al., 2008). Our study indicated that runoff is predicted to increase from the baseline to all three RCPs (Fig. 4d). Increasing runoff may intensify the magnitude and frequency of local floods. More extreme rainfall regimes have beneficial or negative impacts on mesic ecosystems and xeric ecosystems through increasing or decreasing the duration and severity of soil water stress (Knapp et al., 2008). Understanding the direction and amplitude of runoff driven by global warming is necessary to predict how additional ecosystem processes, functions, and services will be altered. Wildfires have a strong impact on biodiversity. Fire is a critical factor in splitting biotas into fire tolerant and intolerant taxa (Bond et al., 2005). Wildfires can greatly reduce biodiversity in temperate and tropical regions but may increase biodiversity in certain fire-dependent ecosystems (Midgley et al., 2010). According to this study, climate change dramatically increases wildfire risk (Fig. 4, Fig. 5j-l, Supplementary Tables 2–4). Under these circumstances, the areas of C_4 grasslands and savannas in South America and Africa would expand under future climate scenarios, and consequently forests would be restrained in these regions (Bond et al., 2005). Our simulation showed that climate change greatly resulted in habitat transformation (Fig. 4, Fig. 5 m-o). Some species may benefit from the expansion of ranges due to global warming, whereas some species would likely be harmed by habitat transformation.

The impacts of climate change and habitat degradation on biodiversity are complex and varied, however, the majority of current studies predict alarming consequences of changing climate on biodiversity (Bellard et al., 2012). Integrated with our study, the boundary, conservation status, and management measures of current ecoregion scheme should be further evaluated and updated for a changing climate.

In the present study, we did not explicitly consider the impacts of human-induced changes to land use or land cover (LULC) or the effects of other types of climate change metrics (e.g., Garcia et al., 2014) on the ecoregions. Therefore, because human-induced changes to LULC would likely increase the impact of our simulation (Newbold et al., 2016; Smith et al., 2016), we believe that our predictions are relatively conservative. Given the relatively small-magnitude but consistent impacts of climate change, it is important to systematically study the trajectories of negative effects on ecosystems; future research should also implement integrated analyses of the implications of ecoregion-level dynamics that are synergistically affected by climate change and LULC. Advances in coupled vegetation-climate modeling will also improve climate change prediction reliability.

5. Conclusions

Our findings indicate that climate change as defined by shifted means and extremes of temperature, precipitation, and cloud cover lead to both significant gains and losses in ecosystem functions. Under future climate scenarios, the mean NPP for all ecoregions is predicted to increase, as is heterotrophic respiration, resulting in a decreased carbon sink under RCP 2.6 and RCP 4.5, but an increased carbon sink under RCP 8.5 due to higher concentrations of carbon dioxide fertilization. Runoff is predicted to increase in all ecoregion categories, but the risk of wildfire and habitat transformation is predicted to increase. Mean and extreme temperature, precipitation, and cloud cover values as well as their interactions were significant drivers affecting the dynamics of five ecological indicators: NPP, carbon storage, runoff, wildfire risk, and habitat transformation. The dynamics of climate change metrics and the five ecological indicators as well as their combination have significant implications for promoting biodiversity conservation in a changing climate. However, because the current ecoregion scheme only includes ecoregion-level presence/absence data for terrestrial amphibians, reptiles, birds, and mammals, the appropriateness of current ecoregion scheme for conserving biodiversity in a changing climate should be evaluated further. Species-specific adaptation measures to climate change should be included or updated.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.04.006.

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