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Original Research Article

Vulnerability of global forest ecoregions to future climate change

Chun-Jing Wang [a, b, c], Zhi-Xiang Zhang [d], Ji-Zhong Wan [a, c, *]

[a] State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining, 810016, China
[b] College of Agriculture and Animal Husbandry, Qinghai University, Xining, 810016, China
[c] Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile
[d] School of Nature Conservation, Beijing Forestry University, Beijing, 100083, China

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A B S T R A C T

The vulnerability of global forest ecoregions to future climate change represents a major threat to biodiversity and ecosystems worldwide. Therefore, it is important to investigate this vulnerability to improve the global conservation management network for biodiversity and ecosystems. We used species–area relationship coupled with correlative distribution modelling to conduct a global vulnerability assessment on 387 forest ecoregions under future climate change across different (1) biomes, (2) biogeographical realms and (3) conservation statuses. We found that 8.8% of global forest ecoregions were highly vulnerable in a low-greenhouse-gas-concentration scenario, and 32.6% of the global forest ecoregions were highly vulnerable in the high-greenhouse-gas-concentration scenario. Furthermore, the overall vulnerability of forest ecoregions was significantly greater for the high-rather than the low-greenhouse-gas-concentration scenario. In particular, critical or endangered forest ecoregions of Temperate Broadleaf and Mixed Forests, Temperate Conifer Forests, Tropical and Subtropical Dry Broadleaf Forests and Tropical and Subtropical Moist Broadleaf Forests were highly vulnerable in Nearctic, Neotropic and Palearctic realms. Furthermore, relatively stable and intact Tropical and Subtropical Moist Broadleaf Forests may be threatened in Neotropic and Afrotropic realms due to their climate change vulnerability. Hence, due to increasing greenhouse gas concentrations, future climate change must be incorporated into forest ecoregion conservation management to improve the effectiveness of global conservation network systems for biodiversity and ecosystems.

1. Introduction

Ecoregions include a distinct assemblage of species and habitats (Olson et al., 2001). Hence, conservation strategies can be considered where biogeographic units are used at the ecoregion scale for biodiversity conservation (Olson et al., 2001). Of all global ecoregions, forest ecoregions contain the largest biodiversity (Olson et al., 2001; Jenkins and Joppa, 2009). Furthermore, forest ecoregions markedly contribute to the diversity of ecosystem services (e.g., maintaining carbon storage, regulating water balance and serving as genetic reserves; Naidoo et al., 2008; Veldman et al., 2015; Da Ponte et al., 2017). However,

* Corresponding author. State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining, 810016, China.
E-mail address: wan1276@163.com (J.-Z. Wan).

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climate change can alter phenology, interactions, species distribution, morphology and net primary productivity in forest ecoregions worldwide (Scheffers et al., 2016; Liu et al., 2018). Thus, it has the strong potential to decrease both the amount and areas of natural resources in forest ecoregions (Beaumont et al., 2011; Watson et al., 2013; Seidl et al., 2014, 2016; Hautier et al., 2015).

Furthermore, future climate change is likely to enhance relevant negative effects on forest ecoregions, and biodiversity and ecosystem services will be threatened by climate change (Seidl et al., 2011, 2014, 2016). Future climate change may lead to a high risk of abrupt and irreversible regional-scale shifts in forest ecoregion composition, structure and function (Beaumont et al., 2011; Pacifici et al., 2015; Wan et al., 2017a). Eigenbrod et al. (2015) demonstrated that global ecosystems may face extreme climatic conditions and be under substantial climatic stress in the future. Thus, biodiversity and ecosystem services will be threatened by future climate change. Hence, the question about how to integrate future climate change into effective forest ecoregion management practices is an urgent necessity to achieve biodiversity conservation and maintain ecosystem services worldwide.

To improve the understanding of management practices, especially when considering forest ecoregions, the vulnerability of global forest ecoregions to future climate change must be assessed (Watson et al., 2013; Pacifici et al., 2015). Numerous assessment approaches, both ongoing as well as projected nearly 100 years into the future, have been developed to determine the vulnerability of species populations, communities and ecosystems to future climate change (Beaumont et al., 2011; Watson et al., 2013; Pacifici et al., 2015; Cianfrani et al., 2018). Pacifici et al. (2015) showed that a regional vulnerability assessment of climate change can be based on distributional changes, extinction probabilities, vulnerability indices and species loss.

The species–area relationship (SAR) can predict biodiversity and ecosystem vulnerability due to species loss caused by climate disappearance based on the species–area accumulation curve (Thomas et al., 2004; Bellard et al., 2014; Matias et al., 2014). Previous studies (e.g., Thomas et al., 2004; Bellard et al., 2014; Keil et al., 2015; Deane et al., 2017) used the SAR to assess vulnerability of biodiversity as a consequence of rapid climate change. Correlative distribution modelling (CDM) refers to modelling used to project population and vegetation distribution areas; it is based on presence points and relevant environmental variables. It has also been used to assess the vulnerability of biodiversity hotspots, vegetation and plant communities to future climate change (Bellard et al., 2014; Soto-Berelov et al., 2015; Ullerud et al., 2016; Wang et al., 2017a,b; Wan et al., 2017a). Furthermore, climatic variables are the main factors that control the distribution and composition of forest vegetation, and climatic regions can provide a basis for global forest vulnerability assessments (Kinzig and Harte, 2000; Eigenbrod et al., 2015). Hence, the existing assessment approaches can support the vulnerability of global forest ecoregions to future climate change. Once this vulnerability assessment is established, researchers can create a link between an explicitly stated expectation about global warming and effective forest ecoregion management (Millar et al., 2007; Seidl et al., 2011; Watson et al., 2013). Then, the effectiveness of forest ecoregion management practices may be enhanced towards future climate change (Watson et al., 2013; Pacifici et al., 2015).

Based on a study by Olson et al. (2001), a series of forest ecoregions across different biomes and biogeographical realms worldwide were selected for their irreplaceability or distinctiveness; this selection represents an ambitious blueprint for global conservation. Intensive human activities, forest degradation, habitat fragmentation and urbanisation can affect forest areas, and these changes are highly related to biodiversity loss. We should avoid effects of human disturbances on SAR. Hence, natural forested areas could be used as key indicators for the assessment of species diversity loss across disparate spatial scales (Kinzig and Harte, 2000; Gonzalez et al., 2010; Eigenbrod et al., 2015). Here, we evaluated the vulnerability of global forest ecoregions to future climate change using SAR, based on the relationships between species diversity and natural forest areas.

The objective of our study was to assess the vulnerability of global forest ecoregions to future climate change, and adaptation planning was proposed based on the vulnerability assessment. We used CDM to project the loss of predicted forest areas in ecoregions based on forest areas across different (1) biomes, (2) biogeographical realms and (3) conservation statuses. A crucial hypothesis is that the forest distribution area can define the number of restricted species according to SAR (Kinzig and Harte, 2000; Gonzalez et al., 2010; Bellard et al., 2014; Eigenbrod et al., 2015). There is a positive relationship between the forest distribution area and the number of restricted species within an ecoregion (Kinzig and Harte, 2000). The number of restricted species potentially threatened by climate change can be measured by the extent of the analogue climate loss (Bellard et al., 2014). Based on this hypothesis, we used the relationship between the forest region area (i.e., the forest distribution ranges) and the number of restricted species for the vulnerability assessment on global forest ecoregions under future climate change (Kinzig and Harte, 2000; Gonzalez et al., 2010; Eigenbrod et al., 2015). We used CDM to predict the loss of forest distribution areas in ecoregions. We utilised SAR to evaluate the vulnerability of global forest ecoregions to future climate change by calculating the loss of forest distribution areas. Finally, effective conservation management suggestions were proposed based on the results of vulnerability assessments across different biomes, biogeographical realms and conservation status (detailed information can be found in Fig. 1).

2. Materials and methods

2.1. Current distribution of forest areas in ecoregions

We obtained digital data on global forest ecoregions from Olson et al. (2001). The utilised raster data on the global forest areas was extracted from the Gonzalez et al., 2010 land cover map (http://due.esrin.esa.int/page_globcover.php) via ArcGIS

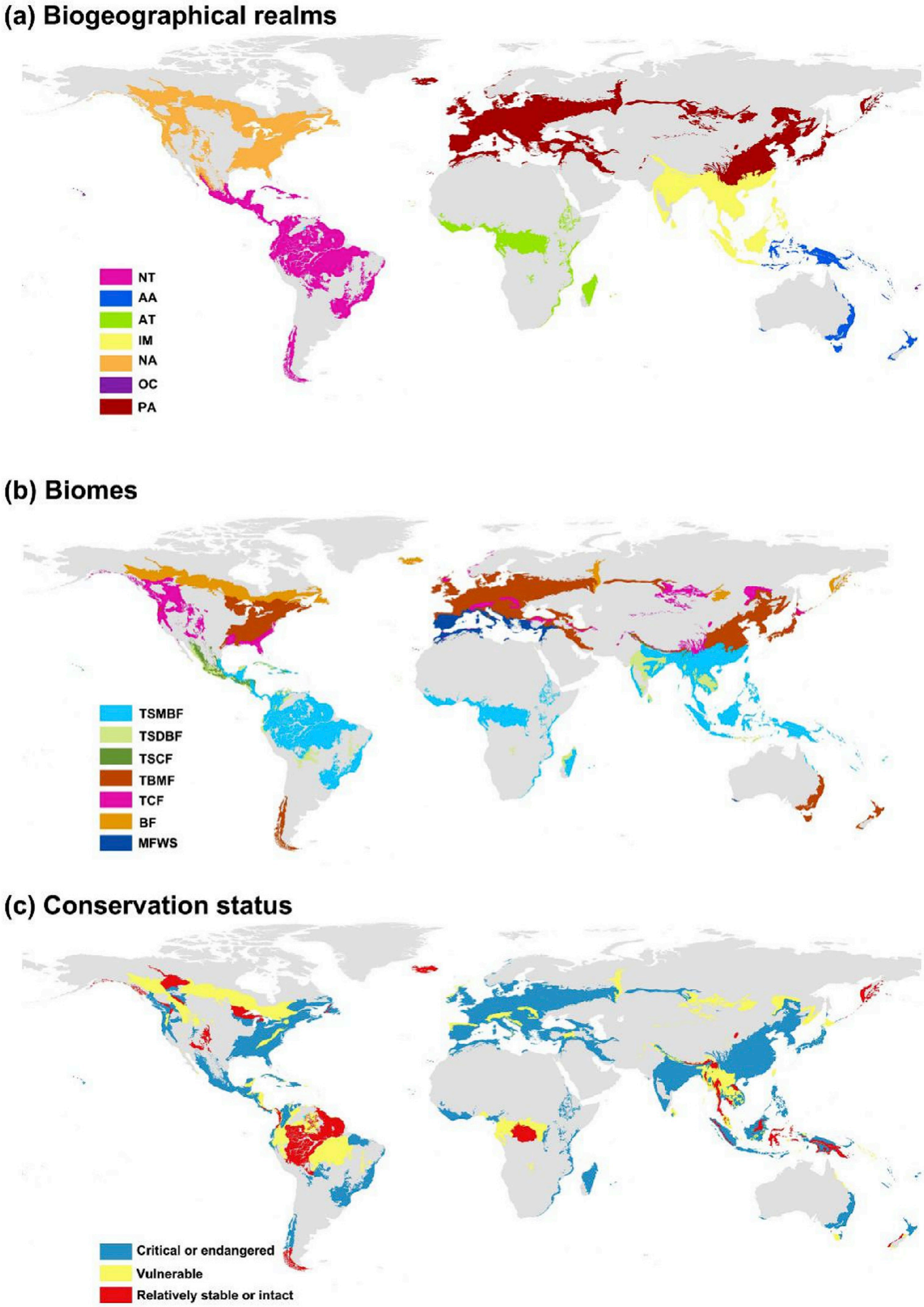

Fig. 1. Ecoregion maps based on seven biogeographical realms, seven biomes and three conservation statuses. (a) Realms: AA, Australasia; AN, Antarctic; AT, Afrotropics; IM, Indomalay; NA, Nearctic; NT, Neotropics; OC, Oceania; PA, Palearctic. (b) Biomes: TSMBF, Tropical and Subtropical Moist Broadleaf Forests; TSDBF, Tropical and Subtropical Dry Broadleaf Forests; TSCF, Tropical and Subtropical Coniferous Forests; TBMF, Temperate Broadleaf and Mixed Forests; TCF, Temperate Conifer Forests; BF, Boreal Forests/Taiga; MFWS, Mediterranean Forests, Woodlands and Scrub. (c) Conservation status: critical or endangered, vulnerable and relatively stable or intact.

10.5 (ESRI, Redlands, CA). The raster data of the global forest areas was transferred into a 10.0 arcmin grid map. We quantified the current forest distribution areas based on the number of grid cells occupied by forests (i.e., their occurrence points were input for the CDM). To produce useful predictions for the CDM, ecoregion types with less than 10 grid cells with forest areas were not included in our study (Meyer et al., 2016).

Our study included 387 forest ecoregions that belong to eight biogeographical realms (Australasia, Antarctic, Afrotropics, Indomalay, Nearctic, Neotropics, Oceania and Palearctic) and seven biomes (Tropical and Subtropical Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests, Tropical and Subtropical Coniferous Forests, Temperate Broadleaf and Mixed Forests, Temperate Conifer Forests, Boreal Forests/Taiga and Mediterranean Forests, Woodlands and Scrub; Olson et al., 2001). Forest ecoregions are distinguished by climate: conifers based on gymnosperm species, broadleaf based on angiosperm species and mixed that include broadleaves and conifers (Olson et al., 2001). Mediterranean Forests, Woodlands and Scrub feature dry summers and rainy winters (Olson et al., 2001). These 387 ecoregions were classified as one of three conservation statuses: "critical or endangered", "vulnerable" or "relatively stable or intact"; classification was based on landscape characteristics, including total habitat loss, habitat fragmentation, degree of degradation, degree of protection needed and degree of urgency for conservation needs (Olson and Dinerstein, 1998). Ecological landscapes are threatened at the highest levels in the critical or endangered ecoregions, whereas the landscapes of the relatively stable or intact ecoregions are threatened the least (Olson and Dinerstein, 1998). Detailed information appears in Table S1 and Fig. 1.

2.2. Future forest distribution areas in ecoregions

We selected 10 climate variables with 10.0 arcmin spatial resolution to build the CDM for forest distribution areas in ecoregions. These 10 climate variables without multicollinearity (with absolute values of correlation coefficient < 0.75) included Annual Mean Temperature, Mean Diurnal Range (monthly mean [max temp - min temp]), Isothermality (mean diurnal range/temperature annual range) x 100), Temperature Annual Range (max temperature of warmest month - min temperature of coldest month), Mean Temperature of Wettest Quarter, Annual Precipitation, Precipitation of Driest Month, Precipitation Seasonality (coefficient of variation), Precipitation of Warmest Quarter and Precipitation of Coldest Quarter. These metrics reflect annual trends and seasonality; extremes can reflect the forest distribution areas. Current variable data were obtained from the WorldClim database (averages from 1950 to 2000 were used as current climate variables; www.worldclim.org), and future climate variable data (namely, 2080s [2071–2099]) were based on from the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5; www.ccafs-climate.org). To project future forest distribution areas, five general circulation models (cccma_canesm2, csiro_mk3_6_0, bcc_csm1_1, mpi_esm_lr and mohc_hadgem2_es) were averaged. Two greenhouse gas concentration scenarios were considered: the low- and high-greenhouse-gas-concentration scenarios (i.e., the Representative Concentration Pathways (RCPs) 4.5 and 8.5, respectively; www.ccafs-climate.org; Meinshausen et al., 2011; Van Vuuren et al., 2011).

Based on the climatic equilibrium scenario for forests (Maiorano et al., 2013; Pearson et al., 2013), we used MaxEnt modelling, a common CDM, to predict the future forest distribution areas in ecoregions based on bioclimatic variables and the current forest distribution areas (Tarkesh and Jetschke, 2012; Wang et al., 2017a,b; Phillips et al., 2006, 2017; Wan et al., 2017a). We excluded the areas significantly influenced by humans based on the Gonzalez et al., 2010 land cover map (http://due.esrin.esa.int/page_globcover.php). MaxEnt is a program for CDM that uses presence-only records (the current forest distribution areas in our study; Tarkesh and Jetschke, 2012; Phillips et al., 2017). Here, (1) we set the regularisation multiplier (beta) at two (Radosavljevic and Anderson, 2014); (2) we used a five-fold cross-validation approach to avoid the bias of occurrence points (Merow et al., 2013); (3) we set 10000 for the maximum number of background points, close to the overall forest distribution for each ecoregion (Merow et al., 2013); (4) we used the cloglog output format for future distribution probabilities (Phillips et al., 2017); (5) other settings were shown as described in Wang et al. (2017a) and Wan et al. (2017a). The "10th percentile training presence threshold" was applied to determine future forest distribution and non-distribution areas for all ecoregions under climate change (Wan et al., 2017a).

The area under the receiver operating characteristic curve (AUC) and training omission rate were used to evaluate the MaxEnt modelling performance (Phillips et al., 2006). The range of AUC values generally varies from 0.5 (worst modelling performance) to 1 (best modelling performance; Phillips et al., 2006). The training omission rate showed the proportion of the correctly predicted points (from MaxEnt modelling) on true distribution areas by using binomial probability (Phillips et al., 2006). The binomial probabilities were based on six thresholds (i.e., Fixed cumulative value 5, Fixed cumulative value 10, Equal training sensitivity and specificity, Maximum training sensitivity plus specificity, Balance training omission, predicted area and threshold value and Equate entropy of thresholded and original distributions; Phillips et al., 2006). We considered modellings as accurate when the AUC was above 0.7 and the training omission rate was below 17%. In our study, the MaxEnt modelling predictions were accurate across all forest ecoregions (Table S1; Phillips et al., 2006).

2.3. Assessing the vulnerability of global forest ecoregions to future climate change

Species restricted to specific climates may disaggregate or disappear due to the specific climate changes in those ecoregions (Beaumont et al., 2011). We evaluated the lost percentage of the forest distribution ranges to quantify the vulnerability of each forest ecoregion to climate change using the following equation (Kinzig and Harte, 2000):

$$V_{lost} = \left(\frac{A_{lost}}{A_{current}}\right)^{z'},$$

where V_{lost} represents the degree of vulnerability of a forest ecoregion to future climate change, $A_{current}$ represents the current distribution areas of the forests in a ecoregion, A_{lost} represents the lost distribution areas of forests in an ecoregion under future climate change (current - future distribution areas) and z′ represents a constant [$z' = -\ln(1-1/2^{z})/\ln(2)$]. To avoid errors and bias due to the grid cell scales, we used 90% confidence limits for V_{lost}. An intermediate z value (0.2) can represent a balance between fragmented and continental habitats, based on the study of Kinzig and Harte (2000). An ecoregion with a value of 1 implies the highest vulnerability scores due to future climate change, and an ecoregion with a value of 0 has the lowest vulnerability due to future climate change (Kinzig and Harte, 2000; Eigenbrod et al., 2015). Based on Eigenbrod et al. (2015), we used the same thresholds for the vulnerability of each forest ecoregion to climate change: very low ($V_{lost} < 0.05$), low ($0.05 \le V_{lost} < 0.2$), medium ($0.2 \le V_{lost} < 0.8$), high ($0.8 \le V_{lost} < 0.95$) and very high ($V_{lost} \ge 0.95$). Such vulnerability assessments were based on seven biogeographical realms, seven biomes and three conservation statuses.

3. Results

Our results showed that the vulnerabilities of 34 forest ecoregions (8.8% of the 387 ecoregions) were high or very high in the low-greenhouse-gas-concentration scenario, while 126 forest ecoregions (32.6% of the 387 ecoregions) were highly vulnerable in the high-greenhouse-gas-concentration scenario (Table S1). This data indicates that the overall vulnerability of forest ecoregions to future climate change was significantly higher in the high-compared to the low-greenhouse-gas-concentration scenario (Fig. 2). Specially, the Tropical and Subtropical Moist Broadleaf Forest ecoregions were highly vulnerable in Afrotropic and Neotropic realms (Table 1). Boreal Forests/Taiga of the Nearctic realm were also highly vulnerable (Table 1). Temperate Broadleaf and Mixed Forests and Temperate Conifer Forests included highly vulnerable forest ecoregions in Nearctic and Palearctic realms (Table 1).

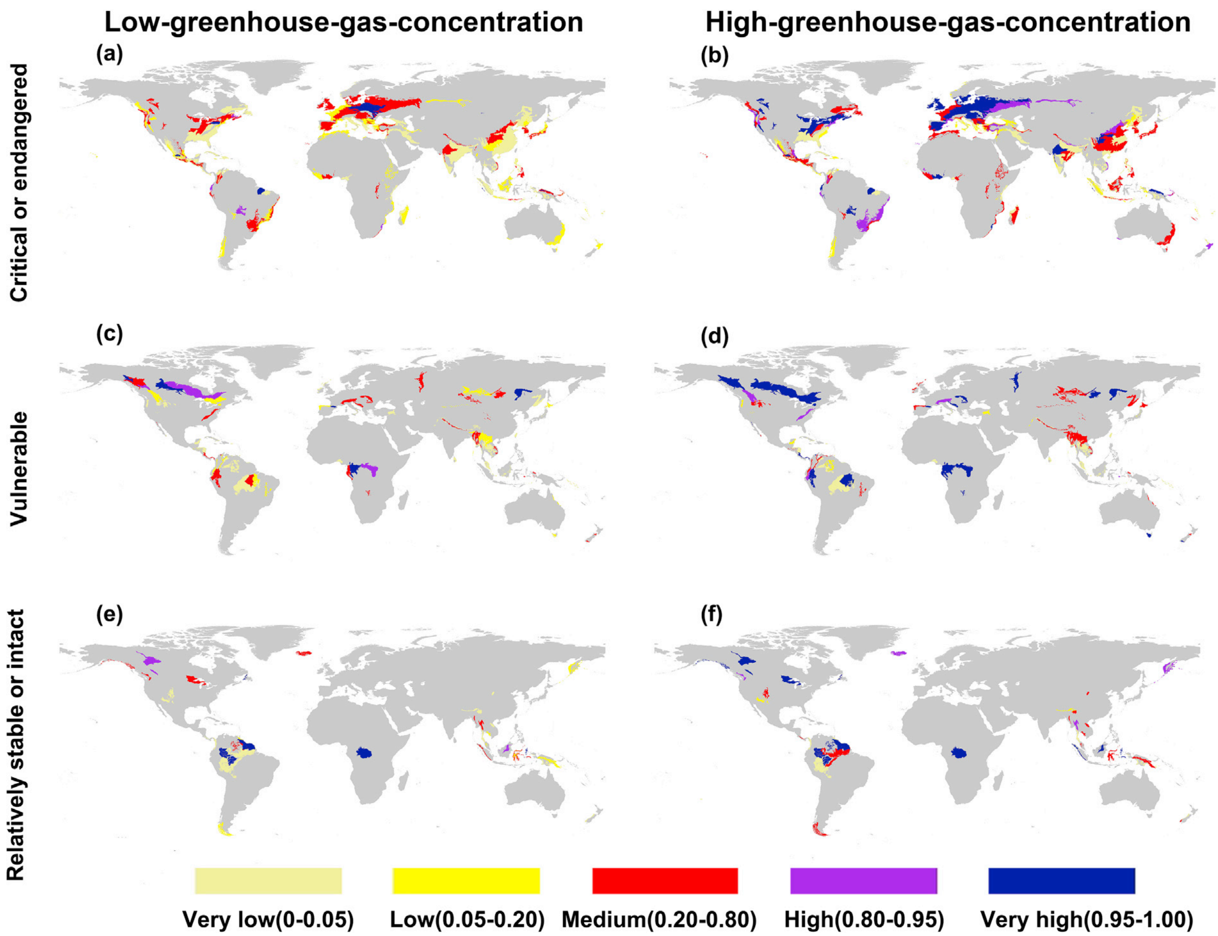

Fig. 2. Vulnerability of global forest ecoregions to future climate change across three conservation statuses and in response to low- (left panels) and high- (right panels) greenhouse-gas-concentration scenarios (a and b for critical or endangered ecoregions; c and d for vulnerable ecoregions; e and f for relatively stable or intact ecoregions).

Table 1
Vulnerability assessment of global forest ecoregions to future climate change based on biogeographical realms and biomes.

Realm	Biome	Very low (0–0.05)	Low (0.05–0.20)	Medium (0.20–0.80)	High (0.80–0.95)	Very high (0.95–1.00)
AA	MFWS	0/0	1/0	0/0	0/1	0/0
AA	TBMF	5/3	5/0	2/5	0/1	0/3
AA	TSDBF	2/1	0/1	1/1	0/0	0/0
AA	TSMBF	6/4	8/3	6/9	0/2	2/4
AT	TSDBF	2/2	0/0	1/0	0/0	0/1
AT	TSMBF	8/5	7/1	4/10	2/1	4/8
IM	TBMF	2/0	0/2	1/1	0/0	0/0
IM	TCF	2/1	0/0	0/1	0/0	0/0
IM	TSCF	1/1	0/0	2/2	0/0	0/0
IM	TSDBF	7/8	1/0	3/0	0/1	0/2
IM	TSMBF	41/36	10/2	10/20	1/2	1/3
NA	BF	1/0	0/0	1/1	3/0	3/7
NA	TBMF	6/4	2/1	7/1	1/2	1/9
NA	TCF	8/2	5/4	11/5	2/4	0/11
NA	TSCF	1/0	0/1	1/1	0/0	0/0
NA	TSDBF	1/1	0/0	0/0	0/0	0/0
NT	TBMF	0/0	2/1	0/1	0/0	0/0
NT	TSCF	3/2	2/1	2/4	0/0	0/0
NT	TSDBF	14/11	4/1	3/5	3/3	1/5
NT	TSMBF	28/16	10/5	15/14	1/11	5/13
OC	TSDBF	2/2	0/0	0/0	0/0	0/0
OC	TSMBF	0/0	2/0	0/2	0/0	0/0
PA	BF	0/0	1/0	3/0	0/2	0/2
PA	MFWS	10/5	3/4	6/4	0/3	0/3
PA	TBMF	18/8	7/5	15/14	0/3	2/12
PA	TCF	8/1	4/3	7/10	0/2	2/5
PA	TSMBF	0/0	2/0	0/2	0/0	0/0

See Fig. 1 legend for a description of the abbreviations. Realms: AA, Australasia; AN, Antarctic; AT, Afrotropics; IM, Indomalay; NA, Nearctic; NT, Neotropics; OC, Oceania; PA, Palearctic. Biomes: TSMBF, Tropical and Subtropical Moist Broadleaf Forests; TSDBF, Tropical and Subtropical Dry Broadleaf Forests; TSCF, Tropical and Subtropical Coniferous Forests; TBMF, Temperate Broadleaf and Mixed Forests; TCF, Temperate Conifer Forests; BF, Boreal Forests/Taiga; MFWS, Mediterranean Forests, Woodlands and Scrub. The values left of the "/" represent the vulnerability assessment of global forest ecoregions in the low greenhouse gas concentration scenario, while the values right of the "/" represent the vulnerability assessment of global forest ecoregions in the high greenhouse gas concentration scenario.

Of forest ecoregions at critical or endangered status, 3.6% were highly vulnerable in the low-greenhouse-gas-concentration scenario, while 18.6% were highly vulnerable in the high-greenhouse-gas-concentration scenario (Table S1). These highly vulnerable ecoregions included the Temperate Broadleaf and Mixed Forests, Temperate Conifer Forests, Tropical and Subtropical Dry Broadleaf Forests and Tropical and Subtropical Moist Broadleaf Forests (Table 2). They were mainly distributed in Nearctic, Neotropic and Palearctic realms, with a particular emphasis on the high-greenhouse-gas-concentration scenario (Table 3).

Table 2
Vulnerability assessment of global forest ecoregions to future climate change based on biomes and conservation statuses.

Biome	Conservation status	Very low (0–0.05)	Low (0.05–0.20)	Medium (0.20–0.80)	High (0.80–0.95)	Very high (0.95–1.00)
BF	Critical or endangered	1/0	0/0	0/1	0/0	0/0
BF	Vulnerable	0/0	0/0	3/0	2/0	2/7
BF	Relatively stable or intact	0/0	1/0	1/0	1/2	1/2
MFWS	Critical or endangered	9/4	4/4	6/4	0/4	0/3
MFWS	Vulnerable	1/1	0/0	0/0	0/0	0/0
TBMF	Critical or endangered	21/13	12/6	20/15	1/5	2/17
TBMF	Vulnerable	5/0	3/1	4/5	0/1	1/6
TBMF	Relatively stable or intact	5/2	1/2	1/2	0/0	0/1
TCF	Critical or endangered	7/3	5/2	10/6	0/3	1/9
TCF	Vulnerable	8/1	4/4	6/8	1/2	1/5
TCF	Relatively stable or intact	3/0	0/1	2/2	1/1	0/2
TSCF	Critical or endangered	4/2	2/2	4/6	0/0	0/0
TSCF	Vulnerable	1/1	0/0	1/1	0/0	0/0
TSDBF	Critical or endangered	23/21	5/2	7/5	3/4	1/7
TSDBF	Vulnerable	4/3	1/0	1/2	0/0	0/1
TSMBF	Critical or endangered	54/39	20/8	17/29	2/13	3/7
TSMBF	Vulnerable	20/18	10/2	12/13	1/2	1/9

See Fig. 1 legend for a description of the abbreviations. Biomes: TSMBF, Tropical and Subtropical Moist Broadleaf Forests; TSDBF, Tropical and Subtropical Dry Broadleaf Forests; TSCF, Tropical and Subtropical Coniferous Forests; TBMF, Temperate Broadleaf and Mixed Forests; TCF, Temperate Conifer Forests; BF, Boreal Forests/Taiga; MFWS, Mediterranean Forests, Woodlands and Scrub. The values left of the "/" represent the vulnerability assessment of global forest ecoregions in the low greenhouse gas concentration scenario, while the values right of the "/" represent the vulnerability assessment of global forest ecoregions in the high greenhouse gas concentration scenario.

Table 3
Vulnerability assessment of global forest ecoregions to future climate change based on biogeographical realms and conservation statuses.

Realm	Conservation status	Very low (0–0.05)	Low (0.05–0.20)	Medium (0.20–0.80)	High (0.80–0.95)	Very high (0.95–1.00)
AA	Critical or endangered	6/3	7/3	3/6	0/3	1/2
AA	Vulnerable	3/2	2/0	4/3	0/1	0/3
AA	Relatively stable or intact	4/3	5/1	2/6	0/0	0/2
AT	Critical or endangered	9/6	7/1	3/10	1/1	0/2
AT	Vulnerable	1/1	0/0	2/0	1/0	1/4
AT	Relatively stable or intact	0/0	0/0	0/0	0/0	3/3
IM	Critical or endangered	38/35	5/2	9/11	0/2	1/3
IM	Vulnerable	10/10	4/0	4/8	0/0	0/0
IM	Relatively stable or intact	5/1	2/2	3/5	1/1	0/2
NA	Critical or endangered	12/7	5/3	13/6	1/3	1/13
NA	Vulnerable	3/0	2/2	4/1	3/2	2/9
NA	Relatively stable or intact	2/0	0/1	3/1	2/1	1/5
NT	Critical or endangered	25/16	10/6	13/12	4/13	2/7
NT	Vulnerable	14/10	6/2	6/7	0/1	0/6
NT	Relatively stable or intact	6/3	2/0	1/5	0/0	4/5
OC	Critical or endangered	2/2	2/0	0/2	0/0	0/0
PA	Critical or endangered	27/13	12/9	23/19	0/7	2/16
PA	Vulnerable	8/1	4/3	7/10	0/1	2/6
PA	Relatively stable or intact	1/0	1/0	1/1	0/2	0/0

See Fig. 1 legend for a description of the abbreviations. Realms: AA, Australasia; AN, Antarctic; AT, Afrotropics; IM, Indomalay; NA, Nearctic; NT, Neotropics; OC, Oceania; PA, Palearctic. The values left of the "/" represent the vulnerability assessment of global forest ecoregions in the low greenhouse gas concentration scenario, while the values right of the "/" represent the vulnerability assessment of global forest ecoregions in the high greenhouse gas concentration scenario.

Of the forest ecoregions at the vulnerable conservation status, 2.3% were highly vulnerable to climate change in the low-greenhouse-gas-concentration scenario; this value increased (8.5%) in the high-greenhouse-gas-concentration scenario (Table S1). The highly vulnerable biomes included only Tropical and Subtropical Moist Broadleaf Forests (Table 2). The ecoregion distribution ranges with high vulnerability mainly included the Neotropic realm (Table 3).

Of forest ecoregions at relatively stable or intact conservation status, 3.1% were highly vulnerable in the low-greenhouse-gas-concentration scenario, and 5.4% were vulnerable in the high-greenhouse-gas-concentration scenario (Table S1). These ecoregions belonged to Tropical and Subtropical Moist Broadleaf Forests (Table 2). The highly vulnerable ecoregions were mainly distributed in Neotropic and Afrotropic realms, particularly in the high-greenhouse-gas-concentration scenario (Table 3).

4. Discussion

Our findings indicate that future climate change will significantly affect forest ecoregions worldwide. Critical or endangered forest ecoregions were particularly markedly vulnerable is Nearctic, Neotropic and Palearctic realms. We delineated key regions based on seven biogeographical realms, seven biomes and three conservation statuses. Below, we provide adaptation planning suggestions for the conservation of global forest ecoregions.

Forests represent a dominant terrestrial ecosystem across the globe (Olson et al., 2001; Hansen et al., 2013; Dinerstein et al., 2017). Globally, forests provide nearly 75% of the biosphere gross primary productivity and contain high plant diversity (Yuan et al., 2010). Forest ecoregions provide a significant share of ecosystem services (e.g., carbon sequestration and climate regulation, food, raw materials, genetic resources and water and air purification) for humans (Naidoo et al., 2008; Beaumont et al., 2011; Wan et al., 2014; Veldman et al., 2015; Da Ponte et al., 2017). We found that the highly vulnerable ecoregions belonged to Tropical and Subtropical Moist Broadleaf Forests in the Afrotropic and Neotropic realms, Boreal Forests/Taiga in the Nearctic realm and Temperate Broadleaf and Mixed Forests and Temperate Conifer Forests in the Nearctic and Palearctic realms. These projections indicate that the ecosystem services of the above-mentioned forest ecoregions would be potentially threatened in the future. We suggest that Fig. 2 represents an important reference for the adaptation of planning management for global forest ecoregions.

We found that 18.6% of critical or endangered forest ecoregions and 8.5% of vulnerable forest ecoregions were highly vulnerable in the high-greenhouse-gas-concentration scenario indicating that many forest ecoregions at critical or endangered and vulnerable conservation statuses would be sensitive to future climate changes (Kinzig and Harte, 2000; Olson et al., 2001; Jenkins and Joppa. 2009; Eigenbrod et al., 2015). Attention must be focused on the climate vulnerability of ecoregions that belong to the temperate and tropical and subtropical forests in Nearctic, Neotropic and Palearctic realms. Forests in the temperate realm will experience a wide range of variability in temperature and precipitation (Fang et al., 2005; Beaumont et al., 2011; Eigenbrod et al., 2015; Wan et al., 2017a). The climate vulnerability of ecoregions (e.g., temperate and tropical and subtropical forests in Nearctic, Neotropic and Palearctic realms) may result in vapour pressure deficits and evaporation, phenomena that would reduce the water available to plant living (Zhao and Running, 2010; Beaumont et al., 2011).

Previous studies (Olson and Dinerstein, 1998; Holle and Simberloff, 2005; Bréda et al., 2006; Bellard et al., 2013; Hansen et al., 2013) showed that species in temperate forest ecoregions are highly sensitive to human activities; furthermore, biological invasion can extensively and significantly impact native communities. Temperature and precipitation alterations can promote habitat fragmentation and biological invasion across different spatial scales (Bellard et al., 2013, 2014; Hansen et al., 2013;Wang et al., 2017b). Hence, future climate change may lead to habitat fragmentation and increase the possibility of biological invasion; these phenomena will, in turn, render temperate forest ecoregions highly vulnerable (Olson and Dinerstein, 1998; Holle and Simberloff, 2005; Hansen et al., 2013; Eigenbrod et al., 2015). The Tropical and Subtropical Dry Broadleaf Forests and Tropical and Subtropical Moist Broadleaf Forests feature rich species diversity (Olson and Dinerstein, 1998). Dinerstein et al. (2017) demonstrated that tropical and subtropical forests have been systematically protected by global nature reserves to reduce human disturbance. Our results revealed that tropical and subtropical forest ecoregions were highly vulnerable to future climate change. Hence, we should pay attention to the dangers of future climate change coupled with human disturbance in tropical and subtropical forest ecoregions.

Furthermore, the Tropical and Subtropical Moist Broadleaf Forests at relatively stable or intact status should be protected in Neotropic and Afrotropic realms. Both ecosystems, and the biodiversity of such ecoregions, are currently stable, and protected areas retain considerable intact natural habitats. We found that more than 3.1% of global relatively stable or intact forest ecoregions were highly vulnerable under climate change, a projection that indicates a relatively high risk for stable or intact forest ecoregions to become potentially vulnerable (Eigenbrod et al., 2015). Furthermore, Beaumont et al. (2011) demonstrated that climate variability may impose increasingly negative impacts on biodiversity and ecosystems. Hence, relatively stable or intact forest ecoregions that are vulnerable to future climate are not absolutely safe, particularly those located in South and North America and Africa.

In this study, we offer two adaptation planning suggestions. First, conservation decision-making should prioritise actions to satisfy conservation objectives for a set of species and areas based on forest ecoregions that are particularly vulnerable to future climate change (Beaumont et al., 2011; Watson et al., 2013; Wan et al., 2017b). For example, the tropical and subtropical forest ecoregions of Nearctic, Neotropic and Palearctic realms should be considered high priority for global adaptation planning systems. Thus, the species and habitats within the highly vulnerable ecoregions could be monitored more effectively (Eigenbrod et al., 2015; Wan et al., 2019). Second, conservation management should focus (e.g., in a protected area) on forest ecoregions at critical or endangered and vulnerable conservation statues, because both future climate change and ecological landscape damages could negatively affect forest ecoregions (Beaumont et al., 2011; Watson et al., 2013; Wan et al., 2016). For example, Bellard et al. (2013, 2014) showed that climate change will increase biological invasion on a global scale, and Hautier et al. (2015) demonstrated that anthropogenic environmental changes negatively affect ecosystem stability via biodiversity loss. Thus, appropriate adaptation actions (such as invasive species control) should be planned based on future climate change effects (Bellard et al., 2014; Dinerstein et al., 2017; Wang et al., 2017a,b).

The following inherent uncertainties were considered to be associated with our analysis. (1) The quality of the land cover data was not high due to uncertainty in classification accuracy for land cover. However, our study focused on a broad-scale vulnerability assessment rather than fine-scale local efforts. (2) The SAR used in our study is likely to be affected in the future, particularly because z-values may change considering taxonomic groups. Forest areas are good indicators of species habitats and are related to species richness (Kinzig and Harte, 2000). Furthermore, we predicted relative rankings rather than species richness (Eigenbrod et al., 2015). Hence, we used forest areas and only relative ranking methods to conduct vulnerability assessments to decrease the SAR uncertainties (Kinzig and Harte, 2000; Eigenbrod et al., 2015). (3) Our forest intactness analyses are based on current land cover and did not utilise future projections (Eigenbrod et al., 2015). Additionally, boreal and tropical ecoregions have different slopes in the SAR. Future studies should consider the effects of future land cover and different SAR slopes for vulnerability assessment on forest ecoregions due to climate change. (4) There may be some CDM constraints for the prediction of forest distributions (Jarnevich et al., 2015). Although we optimised the Maxent set forest distribution areas in ecoregions, future studies should consider sample size, background/pseudo-absence and absence data, spatial extent, variable selection, evaluation statistics and model transferal in space or time for CDMs (Jarnevich et al., 2015).

5. Conclusions

We identified key regions and biomes of vulnerable forest areas; their spatial information is potentially useful for the adaptation of large-scale management planning for natural forest resources. Considering the conservation status and effects of future climate change on forest ecoregions, we suggest monitoring critical or endangered temperate and tropical and subtropical forests, which we found to be highly vulnerable in Nearctic, Neotropic and Palearctic realms. The overall vulnerability of forest ecoregions to future climate change was significantly higher in the high-compared to the low-greenhouse-gas-concentration scenario. Due to increasing greenhouse gas concentrations, we should integrate future climate change into forest ecoregion adaptation planning management to improve the effectiveness of global biodiversity conservation systems.

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Appendix A. Supplementary data

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References

Beaumont, L.J., Pitman, A., Perkins, S., Zimmermann, N.E., Yoccoz, N.G., Thuiller, W., 2011. Impacts of climate change on the world's most exceptional ecoregions. Proc. Natl. Acad. Sci. 108, 2306–2311.

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., Courchamp, F., 2014. Vulnerability of biodiversity hotspots to global change. Glob. Ecol. Biogeogr. 23, 1376–1386.

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., Courchamp, F., 2013. Will climate change promote future invasions? Glob. Chang. Biol. 19, 3740–3748.

Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Res. 63, 625–644.

Cianfrani, C., Broennimann, O., Loy, A., Guisan, A., 2018. More than range exposure: global otter vulnerability to climate change. Biol. Conserv. 221, 103–113.

Da Ponte, E., Kuenzer, C., Parker, A., Rodas, O., Oppelt, N., Fleckenstein, M., 2017. Forest cover loss in Paraguay and perception of ecosystem services: a case study of the Upper Parana Forest. Ecosyst. Serv. 24, 200–212.

Deane, D.C., Fordham, D.A., He, F., Bradshaw, C.J., 2017. Future extinction risk of wetland plants is higher from individual patch loss than total area reduction. Biodivers. Conserv. 209, 27–33.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminterl, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Nigel, S., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., Souza, N.D., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Pataelt, A., Ghazanfar, S.A., Timberlake, J., Kloser, H., Shennan-farpon, Y., Kindt, R., Lilleso, J.B., van Breugel, P., Graudal, L., Voge, M., AL-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. Bioscience 67, 534–545.

Eigenbrod, F., Gonzalez, P., Dash, J., Steyl, I., 2015. Vulnerability of ecosystems to climate change moderated by habitat intactness. Glob. Chang. Biol. 21, 275–286.

Fang, J., Piao, S., Zhou, L., He, J., Wei, F., Myneni, R.B., Tucker, C.J., Tan, K., 2005. Precipitation patterns alter growth of temperate vegetation. Geophys. Res. Lett. 32, L21411.

Gonzalez, P., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2010. Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. Glob. Ecol. Biogeogr. 19, 755–768.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T., Reich, P.B., 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348, 336–340.

Holle, B.V., Simberloff, D., 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86, 3212–3218.

Jarnevich, C.S., Stohlgren, T.J., Kumar, S., Morisette, J.T., Holcombe, T.R., 2015. Caveats for correlative species distribution modeling. Ecol. Inf. 29, 6–15.

Jenkins, C.N., Joppa, L., 2009. Expansion of the global terrestrial protected area system. Biol. Conserv. 142, 2166–2174.

Keil, P., Storch, D., Jetz, W., 2015. On the decline of biodiversity due to area loss. Nat. Commun. 6, 8837.

Kinzig, A.P., Harte, J., 2000. Implications of endemics–area relationships for estimates of species extinctions. Ecology 81, 3305–3311.

Liu, H., Mi, Z., Lin, L., Wang, Y., Zhang, Z., Zhang, F., Wang, H., Liu, L., Zhu, B., Cao, G., Zhao, X., Sanders, N.J., Classen, A.T., Reich, P.B., He, J., 2018. Shifting plant species composition in response to climate change stabilizes grassland primary production. Proc. Natl. Acad. Sci. 115, 4051–4056.

Maiorano, L., Cheddadi, R., Zimmermann, N.E., Pellissier, L., Petitpierre, B., Pottier, J., Laborde, H., Hurdu, B.I., Pearman, P.B., Psomas, A., Singarayer, J.S., Broennimann, O., Vittoz, P., Dubuis, A., Edwards, M.E., Binney, H.A., Guisan, A., 2013. Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. Glob. Ecol. Biogeogr. 22, 302–317.

Matias, M.G., Gravel, D., Guilhaumon, F., Desjardins-Proulx, P., Loreau, M., Münkemüller, T., Mouquet, N., 2014. Estimates of species extinctions from species–area relationships strongly depend on ecological context. Ecography 37, 431–442.

Meinshausen, M., Smith, S.J., Calvin, K., Daniel, J.S., Kainuma, M.L.T., Lamarque, J.F., Matsumoto, K., Montzka, S.A., Raper, S.C.B., Riahi, K., Thomson, A., Velders, G.J.M., van Vuuren, D.P.P., 2011. Clim. Change 109, 213.

Merow, C., Smith, M.J., Silander, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36, 1058–1069.

Meyer, C., Weigelt, P., Kreft, H., 2016. Multidimensional biases, gaps and uncertainties in global plant occurrence information. Ecol. Lett. 19, 992–1006.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151.

Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R.E., Lehner, B., Malcolm, T.R., Ricketts, T.H., 2008. Global mapping of ecosystem services and conservation priorities. Proc. Natl. Acad. Sci. 105, 9495–9500.

Olson, D.M., Dinerstein, E., 1998. The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. Conserv. Biol. 12, 502–515.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Loucks, C.J., 2001. Terrestrial Ecoregions of the World: a New Map of Life on Earth A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. Bioscience 51, 933–938.

Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E., Butchart, S.H., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., Corlett, R.T., Huntley, B., Bickford, D., Carr, J.A., Hoffmann, A.A., Midgley, G.F., Pearce-Kelly, P., Pearson, R.G., Williams, S.E., Willis, S.G., Young, B., Rondinini, C., 2015. Assessing species vulnerability to climate change. Nat. Clim. Chang. 5, 215.

Pearson, R.G., Phillips, S.J., Loranty, M.M., Beck, P.S., Damoulas, T., Knight, S.J., Goetz, S.J., 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nat. Clim. Chang. 3, 673.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40, 887–893.

Radosavljevic, A., Anderson, R.P., 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. J. Biogeogr. 41, 629–643.

Scheffers, B.R., De Meester, L., Bridge, T.C., Hoffmann, A.A., Pandolfi, J.M., Corlett, R.T., Butchart, S.H., Pearce-Kelly, P., Kovacs, K.M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W.B., Martin, T.G., Mora, C., Bickford, D., Watson, J.E., 2016. The broad footprint of climate change from genes to biomes to people. Science 354, aaf7671.

Seidl, R., Rammer, W., Lexer, M.J., 2011. Climate change vulnerability of sustainable forest management in the Eastern Alps. Clim. Change 106, 225–254.

Seidl, R., Schelhaas, M.J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nat. Clim. Chang. 4, 806.

Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J. Appl. Ecol. 53, 120–129.

Soto-Berelov, M., Fall, P.L., Falconer, S.E., Ridder, E., 2015. Modeling vegetation dynamics in the Southern levant through the Bronze Age. J. Archaeol. Sci. 53, 94–109.

Tarkesh, M., Jetschke, G., 2012. Comparison of six correlative models in predictive vegetation mapping on a local scale. Environ. Ecol. Stat. 19, 437–457.
Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145.
Ullerud, H.A., Bryn, A., Klanderud, K., 2016. Distribution modelling of vegetation types in the boreal–alpine ecotone. Appl. Veg. Sci. 19, 528–540.
Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., Masui, T., 2011. The representative concentration pathways: an overview. Clim. Change 109, 5.
Veldman, J.W., Overbeck, G.E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G.W., Durigan, G., Buisson, E., Putz, E., Bond, W.J., 2015. Where tree planting and forest expansion are bad for biodiversity and ecosystem services. Bioscience 65, 1011–1018.
Wan, J., Wang, C., Yu, J., Nie, S., Han, S., Liu, J., Zu, Y., Wang, Q., 2016. Developing conservation strategies for *Pinus koraiensis* and *Eleutherococcus senticosus* by using model-based geographic distributions. J. For. Res. 27, 389–400.
Wan, J., Wang, C., Yu, J., Nie, S., Han, S., Zu, Y., Chen, C., Yuan, S., Wang, Q., 2014. Model-based conservation planning of the genetic diversity of *Phellodendron amurense* Rupr due to climate change. Ecol. Evol. 4, 2884–2900.
Wan, J.Z., Wang, C.J., Qu, H., Liu, R., Zhang, Z.X., 2017a. Vulnerability of forest vegetation to anthropogenic climate change in China. Sci. Total Environ. 621, 1633–1641.
Wan, J.Z., Yu, J.H., Yin, G.J., Song, Z.M., Wei, D.X., Wang, C.J., 2019. Effects of soil properties on the spatial distribution of forest vegetation across China. Glob Ecol. Conserv. 18, e00635.
Wan, J.Z., Wang, C.J., Yu, F.H., 2017b. Spatial conservation prioritization for dominant tree species of Chinese forest communities under climate change. Clim. Change 144, 303–316.
Wang, C.J., Wan, J.Z., Zhang, Z.X., 2017a. Expansion potential of invasive tree plants in ecoregions under climate change scenarios: an assessment of 54 species at a global scale. Scand. J. For. Res. 32, 663–670.
Wang, S., Xu, X., Shrestha, N., Zimmermann, N.E., Tang, Z., Wang, Z., 2017b. Response of spatial vegetation distribution in China to climate changes since the Last Glacial Maximum (LGM). PLoS One 12, e0175742.
Watson, J.E., Iwamura, T., Butt, N., 2013. Mapping vulnerability and conservation adaptation strategies under climate change. Nat. Clim. Chang. 3, 989.
Yuan, W., Liu, S., Yu, G., Bonnefond, J.M., Chen, J., Davis, K., Desaih, A.R., Goldstein, A.H., Gianelle, D., Rossi, F., Suyker, A.E., Shashi, B., Verma, S.B., 2010. Global estimates of evapotranspiration and gross primary production based on MODIS and global meteorology data. Remote Sens. Environ. 114, 1416–1431.
Zhao, M., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329, 940–943.