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Mapping vulnerability and conservation adaptation strategies under climate change

James E. M. Watson[1,2]*†, Takuya Iwamura[2,3]† and Nathalie Butt[2]

Identification of spatial gradients in ecosystem vulnerability to global climate change and local stressors is an important step in the formulation and implementation of appropriate countermeasures[1,2]. Here we build on recent work to map ecoregional exposure to future climate, using an envelope-based gauge of future climate stability—defined as a measure of how similar the future climate of a region will be to the present climate[3,4]. We incorporate an assessment of each ecoregion's adaptive capacity, based on spatial analysis of its natural integrity—the proportion of intact natural vegetation—to present a measure of global ecosystem vulnerability. The relationship between intactness (adaptive capacity) and stability (exposure) varies widely across ecoregions, with some of the most vulnerable, according to this measure, located in southern and southeastern Asia, western and central Europe, eastern South America and southern Australia. To ensure the applicability of these findings to conservation, we provide a matrix that highlights the potential implications of this vulnerability assessment for adaptation planning and offers a spatially explicit management guide.

Anthropogenic climate change is impacting ecosystems globally, causing changes in phenology, species composition and range shifts[5], while increasing environmental degradation is leading to habitat fragmentation or loss. These two factors in concert are likely to result in exacerbated biodiversity decline and extinction in the near future[6]. As rates of both biodiversity loss and threats are growing[7], the identification of spatial gradients of ecosystem vulnerability to both global and regional drivers is required for the development of effective conservation measures.

There are three shortcomings in present conservation-oriented climate change assessments, regardless of their spatial scale. The first concerns vulnerability assessments, which until recently have been focused solely on the system's (extrapolated from species') exposure to future climate change, without considering that vulnerability to climate change is influenced by the system's (species') sensitivity and adaptive capacity, as well as exposure[1,2,8,9]. For conservation planning purposes, this sole focus on exposure does not always equate to the identification of areas that have the most pressing needs for adaptation, particularly those that may be relatively stable climatically but are far more vulnerable to climate change owing to other reasons (for example, present levels of vegetation intactness). The second shortcoming is that most climate change assessments have been conducted on species-specific responses, and therefore have been largely unable to inform conservation actions in terms of ecosystem-focused adaptation[10,11]. The third shortcoming is that few species or ecosystem assessments have attempted to identify (and map) the specific adaptation action needed to overcome the threats posed by climate change, especially as related to land use and land use change, the other significant driver of ecosystem change. Most research so far provides generic, non-spatially explicit adaptation recommendations (such as corridor development, managed translocations, adaptive management[1,12]), without considering the size and location of each threat. Although generic recommendations are useful, climate change is going to affect ecosystems directly and indirectly in a myriad of non-uniform ways[8,9]. Research is thus needed to identify not only which adaptation activities are necessary above and beyond present conservation activities, but also where they are most appropriate.

Here we produce a methodology to overcome these shortcomings by undertaking an ecoregional assessment at the global scale that integrates an ecoregion's adaptive capacity, based on a spatial analysis of the ecoregion's natural integrity (defined as the proportion of intact natural vegetation found in each ecoregion, and thus a function of land use), with its relative exposure to future climate change, to help inform spatially explicit adaptation guidance for conservation practitioners. Ecoregions were used as the spatial unit of assessment as they are the most relevant environmental and ecologically distinct spatial unit at the global scale[13], and are used widely to guide global conservation investments, assessments and action.

We mapped ecoregional exposure to future climate by using an envelope-based gauge[14] of future climate stability, defined as the similarity between present and future climate[3,4] (2050s; equation (1)). The global distribution of climate stability varied largely among ecoregions (Fig. 1a,b), with a mean climate stability of 42.3% (s.d. = 19.8) and a median of 44.8%. Ecoregions with relatively low climate stabilities tended to be located at high latitudes, such as North America and Europe and southern Patagonia, or at uniformly high altitudes such as the northern Tibetan Plateau (Fig. 1a and Supplementary Information), whereas ecoregions that are climatically more stable showed greater variation in elevation and were located predominantly in low latitudes[4] (Fig. 1a). However, some ecoregions located close to the Equator (for example, northeastern South America) and at low altitudes (for example, southern Australia) were found to have relatively low climate stability (Fig. 1a). Close examination of the relationship between bioclimatic variables and the ecoregional climatic envelopes showed that precipitation of the driest quarter and precipitation seasonality were significant determinants of climate stability (Supplementary Table S1 and Fig. S1a–c). When

[1]Global Conservation Program, Wildlife Conservation Society, Bronx, New York 10460, USA, [2]School of Biological Sciences and School of Geography, Planning and Environmental Management, University of Queensland, St Lucia, Queensland 4072, Australia, [3]Department of Biology and Department of Environmental Earth System Science, Stanford University, Stanford, California 94035, USA. †These authors contributed equally to this work. *e-mail: jwatson@wcs.org

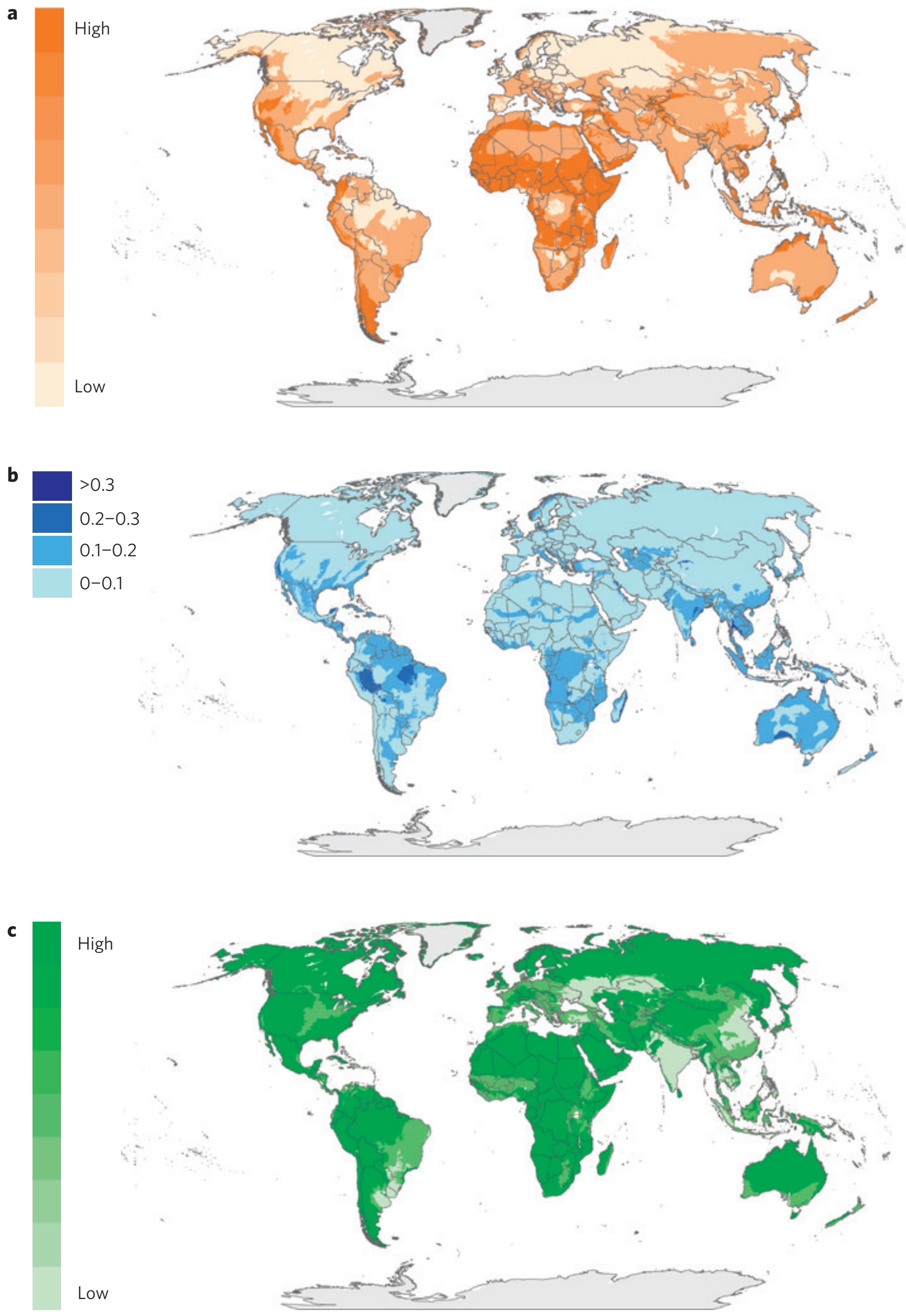

Figure 1 | Terrestrial global distribution of ecoregional climate stability and vegetation intactness. a–c, Terrestrial global distribution of ecoregional climate stability (**a**), standard deviation distribution of ecoregional climate stability (**b**) and vegetation intactness (**c**). Climate stability was defined as a measure of how much of an ecoregion will remain suitable (that is, climatic conditions will remain within present parameters) for the species and ecosystems it contains at present[3,4]. It is therefore a relative scale. The darker colours represent more relatively stable climates (that is, regions more suitable for existing ecosystems). The climate stability shown here is the average over the results from the seven GCMs. The standard deviation allows for an assessment of agreement between the seven GCMs. Light blue colours indicate high agreement between the seven GCMs used and darker blue colours indicate less agreement. Vegetation intactness was calculated using the GlobCover 300 data set[26]. The proportion of areas where native vegetation has been transformed through agricultural development and urbanization in each ecoregion was determined and a measure of vegetation intactness of the ecoregion was calculated. This is a conservative measure of intactness as it does not take into account vegetation degradation. As the data were not normal they have been transformed to a normal distribution by taking the square root values. The darker colours represent more intact ecoregions. As resolution is a problem with global maps, we have provided the same maps at the continental scale in the Supplementary Information.

ecoregional vegetation intactness was assessed, we found that the most degraded ecoregions were located in western Europe, North America, eastern South America, China, India, and southern and southeast Asia (Fig. 1c and Supplementary Information). The relationship between vegetation intactness and relative climate stability varied widely across ecoregions (Fig. 2). The relationship between these two variables was significant ($n = 803$, $p < 0.01$) but weakly negative (Spearman's $\rho = -0.176$).

The degree to which an ecoregion was vulnerable to climate change changed substantially across all inhabited continents when ecoregional integrity was considered (Figs 1a and 2b). This shows the importance of integrating assessments that highlight

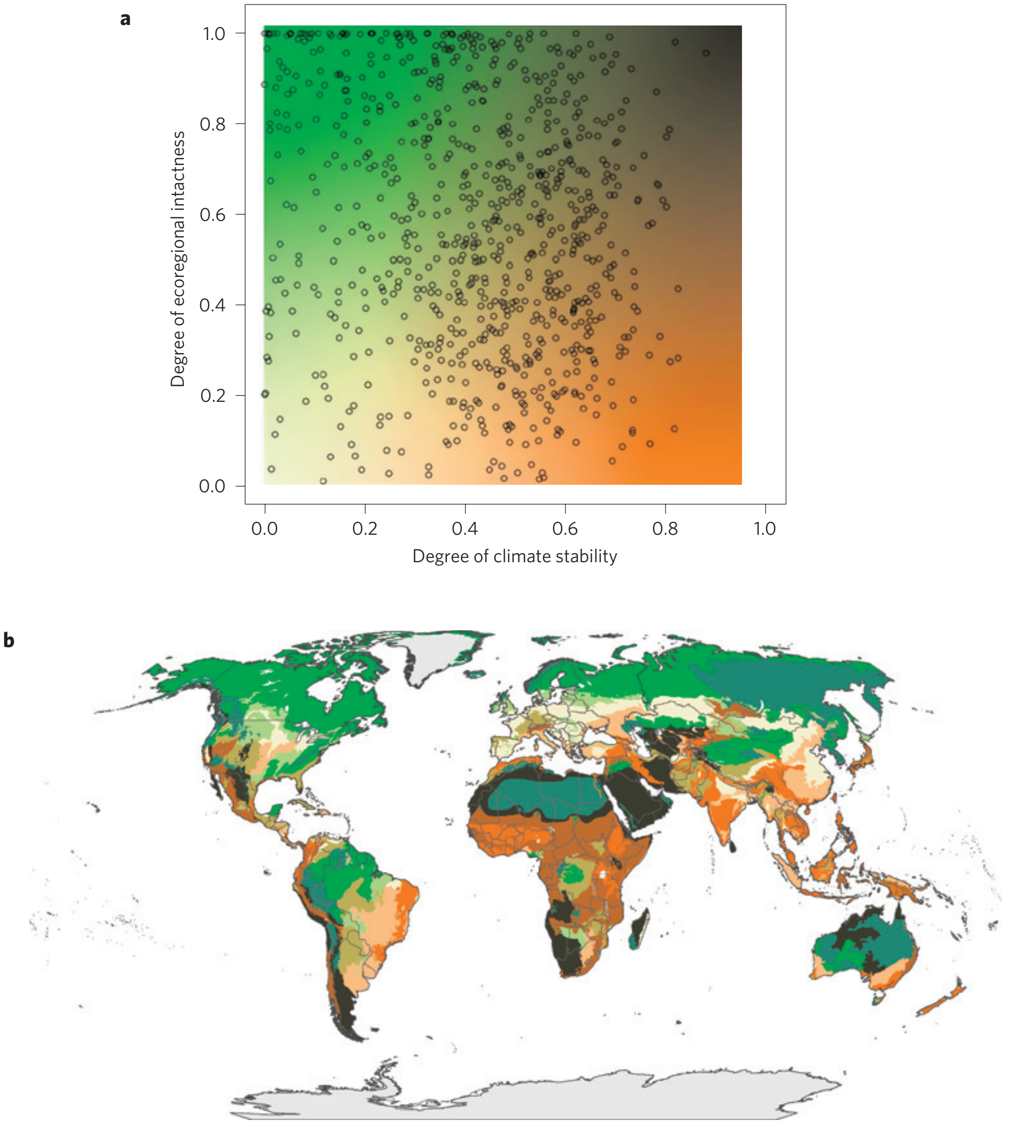

Figure 2 | The relationship between ecoregional climate stability and vegetation intactness. a,b, The relationship between ecoregional climate stability and mean ecoregional intactness ($n = 803$; **a**) and the global distribution of the relationship (**b**). Ecoregions that have high relative climate stability and high vegetation intactness are depicted as dark grey. Ecoregions that have relative high climate stability but low levels of vegetation intactness are depicted in dark orange. Ecoregions that have low relative climate stability but high vegetation intactness are depicted in dark green. Ecoregions that have both low relative climate stability and low levels of vegetation intactness are depicted in pale cream. The intactness axis has been transformed to a normal distribution for presentation purposes by taking the square root values. The colours match the map in **b** and are a combination of the colours in Fig. 1a,b.

future exposure to climate change with those that consider other elements of ecosystem vulnerability (that is, adaptive capacity and sensitivity). For example, when climate stability (as a measure of exposure) is combined with vegetation intactness (as a measure of adaptive capacity), ecoregions located in southwest, southeast and central Europe, India, China and Mongolia, southeast Asia, central North America, eastern Australia and eastern South America were found to be relatively climatically unstable and degraded (Fig. 2b and Supplementary Information). This contrasts sharply with other global assessments (based only on exposure to climate change) that show that central Africa, northern South America and northern Australia are most vulnerable to climate change[3,15,16].

There is strong evidence that climate change is negatively interacting with habitat loss and synergistically contributing to the degradation of biological diversity[17]. We identified, according to our model, ecoregions likely to be future hotspots for biodiversity loss when considering both present levels of landscape transformation and future climate change (Fig. 2b). Owing to their low levels of vegetation intactness and high levels of fragmentation, ecoregions expected to experience very different future climate will probably witness changes in their species assemblages due to loss of the habitat necessary for rapid dispersal or refugial retreat[18].

Beyond identifying future vulnerability based on present ecoregion intactness and climate stability, the approach outlined in this analysis, demonstrated using one scenario and time step, will be better able to help inform adaptation planning than previous global analyses, which assessed vulnerability based solely on predicted exposure to future climate[3,15,16]. By integrating present land use (ecoregional vegetation intactness) into climate change vulnerability assessments, we are able to provide a spatially explicit framework for different broad-scale management strategies and interventions[12] (Table 1 and Fig. 2). Highly intact ecoregions predicted to have a relatively stable climate are unlikely to contain a large suite of species that would require new and radical conservation interventions, such as translocations of species, before the middle of the present century. In these ecoregions, a focus on

Table 1 | Examples of different conservation strategies aimed at increasing ecosystem adaptive capacity, based on the degree of ecoregional intactness and future relative climate stability.

Degree of ecoregional intactness and relative climate stability	Future of ecoregional biodiversity if present land use and non-climate change threats are abated	Example of appropriate ecoregional level science-based strategies, incorporating active adaptive management
High levels of vegetation intactness, high relative climate stability (grey in Fig. 2)	Low numbers of threatened and declining species Low turnover of species within ecoregion due to climate change Functioning ecological processes that will sustain adaptive capacity of species	Identify and manage present direct threats to ensure vegetation remains intact and functional to maintain populations of extant viable species Less emphasis on identifying and protecting/restoring climate refugia, as climate is stable Monitor extant viable species against present threatening processes
High levels of vegetation intactness, low relative climate stability (green in Fig. 2)	Low numbers of threatened and declining species High turnover of species within and beyond ecoregion as species track their climate niche Functioning ecological processes will allow some species to persist in changing climate but adaptive capacity of other species may be exceeded owing to degree of climate change: chance of extinction unless preventative action taken	Manage present direct threats to ensure vegetation is intact to maintain populations of species and their dispersal pathways as they track their climate niche and adapt to changing climate Emphasize the identification and protection of climate refugia Manage present direct threats to ensure vegetation is intact to allow emigrating populations of species to establish themselves Monitor potentially climate-sensitive species and feed this into translocation plans
Low levels of vegetation intactness, high relative climate stability (orange in Fig. 2)	High numbers of threatened and declining species Small turnover of species within ecoregion Reduction in the number of functioning ecological processes, which will severely impact the adaptive capacity of species	Identify and manage present direct threats to ensure vegetation does not lose even more intactness and function to maintain populations of extant viable species Habitat restoration activities aimed at connectivity to increase population size and dispersal capacity of these species. Monitor extant viable species against present threatening processes
Low levels of vegetation intactness, low relative climate stability (cream in Fig. 2)	High numbers of threatened and declining species High turnover of species within and beyond ecoregion as species track their climate niche Reduction in the number of functioning ecological processes, which will severely impact the adaptive capacity of species that may already be exceeded owing to degree of climate change	Manage present direct threats to intact vegetation to maintain populations of species and their dispersal pathways, as they track their climate niche and adapt to changing climate Habitat restoration activities aimed at connectivity to increase population size and dispersal capacity of extant viable species Emphasize the identification and protection of climate refugia Manage present direct threats to ensure vegetation is intact to allow emigrating populations of species to establish themselves Identify the species most vulnerable to climate change and assess translocation options Monitor potentially climate-sensitive species and feed this into translocation plans

management options (for example, the establishment of protected areas) that deal with present threatening processes (for example, invasive species, industrial logging) is sensible, as these processes are likely to have the most serious impact on biodiversity in the short and mid-term[1]. Within ecoregions that are highly intact but are predicted to have a very different climate to the one experienced today, it will be important to reduce threatening processes to ensure that species can take advantage of their capacity to adapt ecologically, albeit retreating to refugia, undergoing a range change as they track the climate, or exhibiting some form of phenotypic plasticity or micro-evolution[19]. However, it is not known how most species will respond to rapid climate change, and in intact but climatically unstable ecoregions, monitoring (linked with adaptation management protocols) is crucial, as it will inform practitioners which species are unlikely to cope with the changes, and are therefore candidates for more aggressive adaptive action (for example, translocation, *ex situ* conservation).

Conversely, in ecoregions that are highly degraded and are likely to have a very different future climate, a strategy that deals only with present threatening processes is short-sighted (Table 1). The identification of potentially vulnerable species and ecosystems in these ecoregions (despite the uncertainty involved) will probably lead to a greater chance of long-term conservation success. It may be appropriate to use a mixture of more proactive management strategies; such as species translocation[20], habitat engineering[6], and restructuring the priorities among conservation options[21]. In those ecoregions that are highly degraded but are predicted to be less affected by large baseline shifts in climatic conditions in the future, there is a need to strengthen efforts aimed at restoration and the removal of other threatening processes.

We do not advocate that no climate adaptation action should be carried out in those ecoregions considered to be relatively highly climatically stable. Indeed, climate change is occurring everywhere on the planet, and there remains large uncertainty around all climate models. All conservation planning must consider the impacts of future climate change: our adaptation matrix highlights the fact that land use and climate change are not spatially uniform and thus different adaptation priorities are needed for different places, depending on the degree of change they have experienced and are likely to experience in future. Although our present analyses are at the ecoregional level, this type of analysis is not limited to this scale (for example, see ref. 22 for a similar biome-scale, multi-thematic analysis). Indeed, as land use decisions are often made at landscape and local scales, and as species track climate change within an ecoregion, these types of assessment could be carried out at much finer scales and include local and regional climatology[23]. It is important to note that although there have been large improvements in climate models over the past decade, associated uncertainty remains high. The climate stability and landscape intactness analyses should be updated for future work as more accurate climate models, emission scenarios and global land use models become available and the analyses can be extended beyond the 2050s. Incorporation of some measure of vegetation change (related to the rate of land degradation), as a function of climate vulnerability, would add great value to future analyses, as such changes are driven by human demography and are very difficult to model.

As biodiversity disruption and loss increase along with intensified climate-change impacts, conservation planners need to move beyond focusing on the long-term future and only on elements of exposure to climate change. Within the context of conservation practice, vegetation intactness is more significant than climate stability for ecosystem vulnerability: in terms of ecosystem degradation or species extinctions, reduction in vegetation intactness is a greater threat than climate change at present, and is likely to be in future, especially in tropical regions[24]. This analysis takes account of the fact that conservation today proceeds in the context of pronounced, and in some places overwhelming, human influence. The development of effective conservation strategies needs to rely not only on improving the knowledge of how species and ecosystems will react to climate change, but also on predicting how humans are going to respond: conservation practitioners will have a much greater chance to influence the intactness of an ecosystem rather than its robustness to future climatic conditions (which can only be changed through international mitigation efforts), and therefore a focus on maintaining ecosystem integrity should always be a primary conservation objective.

Methods

Ecoregions are geographic units based on delineations in taxonomic compositions, inferred evolutionary histories, and shared climatic domains[25]. Here we used spatial information on ecoregional boundaries for the terrestrial ecoregions of the world[13]. Our analysis covered 803 ecoregions (97% of terrestrial ecoregions). The remaining 22 ecoregions were omitted from the analysis as they lacked sufficient GlobCover data or climate data points to conduct a statistically rigorous vegetation intactness assessment (for example, mangrove ecoregions).

Our definition of adaptive capacity relates purely to vegetation intactness, as we are concerned with ecosystem-scale vulnerability. We followed the approach of previous studies[8] and used a very conservative measure of the degree of vegetation intactness in an ecoregion, by quantifying the proportion of areas where native vegetation has been totally transformed through agricultural development and urbanization. This was achieved using the GlobCover data set, a global land cover model that provides land-cover classification[26]. We used GlobCover version 2.1, which has a spatial resolution of 300 m (ref. 27). The GlobCover data set comprises global terrestrial data that define 65 land cover types, categorized into Cultivated Terrestrial Areas and Managed Areas, Natural and Semi-natural Terrestrial Vegetation, Natural and Semi-natural Aquatic Vegetation, Artificial Surfaces and Associated Areas, and Inland Water Bodies. We excluded all areas classified as Cultivated Terrestrial Areas and Managed Lands, and Artificial Surfaces and Associated Areas, with the remaining cells within the ecoregion defined as intact. We then calculated the proportion of an ecoregion that contains these cells against the total number of cells within an ecoregion, and used this to calculate the total proportion of vegetation intactness of the ecoregion (hereafter referred to as ecoregional intactness).

We used a downscaled spatial data set for climate variables at the resolution of 2.5 arc min (approx. 4.6 km at the Equator). Observed spatial databases of bioclimatic variables for present climate were obtained from the WorldClim database[28], which provided 8.48 million data points across all of the ecoregions. From the 19 bioclimatic variables, six variables (annual mean temperature, mean diurnal temperature range, mean annual temperature range, annual precipitation, precipitation seasonality and precipitation of the driest quarter) were used to represent general climate patterns, seasonality, and limiting factors of climatic patterns based on global-scale research. Estimated spatial databases of the same climate variables for the 2050s were downloaded from the International Centre of Tropical Agriculture Downscaling data set[29]. This data set provides high-resolution maps for seven major global circulation models (GCMs) from the Intergovernmental Panel on Climate Change Fourth Assessment Report[30], A1b greenhouse gas emission scenario (see Supplementary Information for discussion). This scenario represents technology-focused rapid economic growth with mixed (fossil and non-fossil) fuel sources, and reflects present economic and developmental activity.

A relative climatic stability index was calculated using the recently introduced method for estimating the overlap between present and future climate envelopes for each ecoregion[4,14]. The two-dimensional envelopes were determined on the basis of the six bioclimatic variables from the present and future climate data sets using principal component analysis. The distribution of the probability density was estimated for each climate using kernel density estimation, where each cell value of the density space represents a unique vector of climatic condition[4]. The degree of overlap between present and future climate was estimated using a niche overlap measurement technique[4,14].

The climatic stability S_i of an ecoregion i was calculated for each of the seven GCMs as follows[4]:

$$S_i = 1 - \frac{1}{2}\left(\sum_{jk} |z_{1ijk} - z_{2ijk}|\right) \quad (1)$$

where z_{1ijk} and z_{2ijk} indicate the probability of climatic condition occurrence, and j and k refer to the cell corresponding to the jth and kth bins of the environmental variables of ecoregion i.

We used Spearman's ρ to run a correlation analysis for the two variables, climate stability and vegetation intactness. The vulnerability assessment for each ecoregion was derived by incorporating the two variables, and therefore includes any uncertainty related to the climate stability model. To understand the nature of the principal component analysis axes, the loadings of the bioclimatic variables were analysed (see Supplementary Information, Table S1 and Fig. S1a–c).

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Author contributions

J.E.M.W. and T.I. designed the analysis; J.E.M.W. and T.I. performed the analysis; J.E.M.W., T.I. and N.B. analysed the results and wrote the paper.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.E.M.W.

Competing financial interests

The authors declare no competing financial interests.