

Vulnerability of ecosystems to climate change moderated by habitat intactness

FELIX EIGENBROD¹, PATRICK GONZALEZ², JADUNANDAN DASH³ and ILSE STEYL¹

¹Centre for Biological Sciences, University of Southampton, Southampton SO17 1BJ, UK, ²Natural Resource Stewardship and Science, U.S. National Park Service, Washington, DC 20005-5905, USA, ³Geography and Environment, University of Southampton, Southampton SO17 1BJ, UK

Abstract

The combined effects of climate change and habitat loss represent a major threat to species and ecosystems around the world. Here, we analyse the vulnerability of ecosystems to climate change based on current levels of habitat intactness and vulnerability to biome shifts, using multiple measures of habitat intactness at two spatial scales. We show that the global extent of refugia depends highly on the definition of habitat intactness and spatial scale of the analysis of intactness. Globally, 28% of terrestrial vegetated area can be considered refugia if all natural vegetated land cover is considered. This, however, drops to 17% if only areas that are at least 50% wilderness at a scale of 48 × 48 km are considered and to 10% if only areas that are at least 50% wilderness at a scale of 4.8 × 4.8 km are considered. Our results suggest that, in regions where relatively large, intact wilderness areas remain (e.g. Africa, Australia, boreal regions, South America), conservation of the remaining large-scale refugia is the priority. In human-dominated landscapes, (e.g. most of Europe, much of North America and Southeast Asia), focusing on finer scale refugia is a priority because large-scale wilderness refugia simply no longer exist. Action to conserve such refugia is particularly urgent since only 1 to 2% of global terrestrial vegetated area is classified as refugia and at least 50% covered by the global protected area network.

Keywords: biodiversity, biome shifts, climate change, habitat fragmentation, habitat loss, land cover, national parks, protected areas, vegetation shifts

Received 26 March 2014 and accepted 11 May 2014

Introduction

Human-induced loss and fragmentation of natural land cover are major causes of the current global biodiversity crisis (Pimm & Raven, 2000; Millennium Ecosystem Assessment, 2005; Butchart *et al.*, 2010), while additive or synergistic impacts of climate change are likely to exacerbate the pressures of habitat loss on species and ecosystems (Jetz *et al.*, 2007; Brook *et al.*, 2008; Pereira *et al.*, 2010; Mantyka-Pringle *et al.*, 2012). In particular, large-scale shifts in vegetation biomes due to climate change have altered boreal, temperate, and tropical ecosystems and future shifts may only leave limited refugia from land use and climate change (Scholze *et al.*, 2006; Gonzalez *et al.*, 2010).

Refugia are habitats to which components of biodiversity retreat, in which they persist, or from which they can potentially expand under changing environmental conditions (Keppel *et al.*, 2012). The identification and protection of refugia from climate change and habitat loss offers an important adaptation strategy to conserve biodiversity. Agencies that manage national

parks and other protected areas need spatial information on the locations of potential refugia and vulnerable areas to effectively prioritize adaptation actions for natural resource management (Baron *et al.*, 2009; Oliver *et al.*, 2012; Alagador *et al.*, 2014).

While numerous efforts have projected the impacts of climate change on future distributions of biodiversity at scales ranging from regional (e.g. Carvalho *et al.*, 2010) to global (e.g. Thomas *et al.*, 2004; Foden *et al.*, 2013), much less research has examined the additive effects of climate change and habitat loss. Most such efforts have analysed synergistic effects at either relatively local scales (e.g. Klausmeyer *et al.*, 2011; Cabral *et al.*, 2013; Ponce-Reyes *et al.*, 2013; Riordan & Rundel, 2014) or globally, but focusing on individual taxa (e.g. Jetz *et al.*, 2007; Visconti *et al.*, 2011), or on the effectiveness of protected areas in the face of climate change (e.g. Hannah *et al.*, 2007; Lee & Jetz, 2008).

In contrast, a recent study (Watson *et al.*, 2013) analysed future vulnerability of ecoregions, rather than species, to climate change at the global scale based both on climate projections and the fraction of natural land cover in each ecoregion. Such an approach has considerable value for proactive conservation strategies as it offers a practical way of identifying refugia (Hodgson

Correspondence: Felix Eigenbrod, tel. +44 2380 597382, fax +44 23 8059 5159, e-mail: f.eigenbrod@soton.ac.uk

et al., 2009; Watson *et al.*, 2013). Although global scenarios of land-use change (Millennium Ecosystem Assessment, 2005) suggest that current patterns of habitat loss may be poor predictors of future climate and land-use change-driven losses (Lee & Jetz, 2008), such possible future losses are not inevitable. Indeed, proactively preventing future habitat losses in intact regions rather than recreating habitat in vulnerable areas offers a potentially very effective climate change adaptation strategy (Hodgson *et al.*, 2009).

Here, we analyse the vulnerability of ecosystems globally to climate change based on current levels of habitat intactness and vulnerability to biome shifts at two spatial scales based on three different measures of intactness. We then use this information to identify the locations of potential large-scale (macro) refugia. While conceptually similar to Watson *et al.* (2013), our analysis builds on existing efforts in five important ways.

First, we ran all analyses at two spatial scales – coarse (48 × 48 km) and medium (4.8 × 4.8 km) – thereby examining scale-dependency, a good practice for large-scale conservation planning (conservation biogeography) (Whittaker *et al.*, 2005).

Second, we quantified the conservation value of remaining natural land cover in all analyses by calculating relative species richness (RSR) scores, which are based on the extent of natural habitat weighted by the species-area relationship (SAR) (Arrhenius, 1921). This is important because the relationship between the extent of habitat (measured by the extent of a given natural land cover) and the number of species it supports is not linear, but rather follows the power-law relationship described by the SAR (Rosenzweig, 1995).

Third, we quantified the effect of changing the definition of habitat intactness on our findings, as there is no single way of identifying the intactness of an ecosystem. We did this by comparing the extent of refugia and areas of high vulnerability at both coarse and medium spatial scales based on RSR scores that were calculated based on the coverage of (i) all natural land cover classes, (ii) areas that were at least 50% wilderness (*sensu* Sanderson *et al.*, 2002), and (iii) areas with at least 50% designated as a protected area. We used these three measures of intactness to capture the generally diminished vulnerability to future habitat losses, and hence to climate change, that characterize both wilderness areas (Boakes *et al.*, 2010) and protected areas (e.g. Hannah *et al.*, 2007; Gillson *et al.*, 2013).

Fourth, we used data on the vulnerability of ecosystems to biome shifts due to climate change (Gonzalez *et al.*, 2010) that use historical climate change trends and future vegetation projections of a dynamic global vegetation model (DGVM) to identify potential refugia. In contrast to the equilibrium climate niche methods

used by Watson *et al.* (2013), DGVMs dynamically model the interactions of biogeography, biogeochemical cycling, and wildfire for every pixel in an analysis area at a time step of days or months.

Finally, the data on the vulnerability of ecosystems to biome shifts due to climate change (Gonzalez *et al.*, 2010) use both historical and projected data, in contrast to Watson *et al.* (2013), who only used future projections. Because vegetation often responds slowly to changes in environmental conditions, a time lag between a change in climate and a shift in vegetation can commit an ecosystem to biome change long before any response manifests itself. Therefore, future vulnerability is partially a function of past climate change. Using historical data account for impacts of climate change that have already occurred. This can provide a more complete assessment of vulnerability than future projections alone.

Materials and methods

Spatial analysis of extent of natural habitat and calculation of relative species richness scores

We quantified the current extent of natural vegetated habitat through spatial analysis of 300 m spatial resolution GlobCover 2009 land cover data (Bontemps *et al.*, 2011), excluding bare land, snow, and ice. We conducted analyses at two spatial scales: medium (4.8 × 4.8 km = 16 × 16 pixels) and coarse (48 × 48 km = 160 × 160 pixels). The coarse spatial scale of 48 × 48 km is the approximate spatial resolution of our climate change vulnerability data. Moreover, high levels of natural vegetated land cover at this scale roughly correspond to sufficient habitat for all but the very largest carnivore species (e.g. Crooks, 2002). The medium spatial scale of 4.8 × 4.8 km is a nested subset of the coarse scale (this is important as our combined climate and habitat vulnerability analyses are by necessity run at the 48 × 48 km scale). Moreover, extensive natural habitat at the 4.8 × 4.8 km scale corresponds to sufficient habitat for at least medium-term persistence of many species (e.g. Findlay & Houlihan, 1997). The medium scale is also fine enough to identify refugia within human-dominated landscapes where coarse-scale refugia are unlikely to occur.

We calculated relative species richness (RSR) scores, based on the SAR, for the most common natural vegetated land cover class of all 300 × 300 m GlobCover pixels within each 4.8 × 4.8 km (medium scale analyses) or 48 × 48 km (coarse-scale analyses) area. RSR is a measure of the number of species of any given taxa for a given extent of the most common natural land cover type relative to the number of species that would be present if the entire pixel consisted of this natural land cover type. The SAR has previously been used to predict how species are affected by loss of natural habitat (e.g. Brooks *et al.*, 1997; Thomas *et al.*, 2004) and we use the same form of this power-law relationship here: $S = cA^z$, where S is species

richness, A is area and c and z are constants. We modified previous applications of the SAR to overcome recent critiques of its application in terrestrial systems (He & Hubbell, 2011; Hanski *et al.*, 2013). First, for the constants c and z , we used the mean values from a recent global meta-analysis of SARs (Sólymos & Lele, 2012) in which $\ln[c] = 1.838$ and $z = 0.228$ for plants, birds, and nonvolant mammal species combined. Second, we did not attempt to predict the actual number of species in each pixel, as such values are highly taxon-specific (e.g. Hanski *et al.*, 2013), but instead calculated the rank order of all pixels relative to each other. We did this by standardizing values between 0 and 1 in all cases. As such, RSR ranges from 0 to 1, with 1 indicating 100% cover of a particular land cover class for a given pixel at the scale of analysis. In this approach, the value of the constant c does not affect our results. This is important because c is highly taxon-dependent if used to predict species richness. Our findings should also be unaffected by possible SAR-based overestimates of extinction (He & Hubbell, 2011) since we are not predicting species richness, but simply relative rankings. We used the same equation of the SAR for all habitat types and scales of analysis as there is no evidence that these factors affect z or c per se. We did not control for the impact that island type (habitat 'island' vs. marine island) can have on the SAR, but again, the impact of this factor is mostly on c (Sólymos & Lele, 2012), which does not affect our results. More generally, a sensitivity analysis (results not shown) using the 90% confidence limits of the global equation of Sólymos & Lele (2012) (the confidence limits quantify the local variation, partially due to land cover types, of the SAR) showed no qualitative differences in the final vulnerability results.

Finally, we set the RSR scores in each pixel at the scale of analysis to 0 if at least 80% of the pixel was covered by anthropogenic cover types, as a recent study has shown that the SAR greatly overestimates species richness when the extent of natural habitat remaining is very small (~10–20% or less natural cover) due to habitat fragmentation effects (Hanski *et al.*, 2013). We did not use the new species fragmented area index proposed by Hanski *et al.* (2013) as it requires species-specific information that is not appropriate for our analyses, which is focused on ecosystems, rather than specific taxa. We considered the mixed irrigated/flooded croplands, croplands, and urban areas to be 100% anthropogenic. We considered the mixed cover classes 'mosaic cropland' and 'mosaic vegetation' to be 60% and 35% anthropogenic, respectively, as per GlobCover estimates (Bontemps *et al.*, 2011).

We calculated RSR for the most abundant natural vegetated land cover type rather than for all natural land cover types in each pixel at the scale of analysis for two reasons. First, we sought to identify the current locations of large intact areas of individual natural land cover types because novel, no-analogue vegetation types may become more common under climate change (Reu *et al.*, 2014) and possibly form mosaics with natural land cover types. Hence, identification of extensive areas of intact natural land cover is important. Second, use of the species-area relationship makes the most sense for a particular land cover type. This is because habitat is a species-specific concept (Wiens, 1989) and the

habitat requirements of most species are likely to correspond to a single major natural habitat type rather than to all natural land cover types in a pixel. We excluded nonvegetated areas as even high amounts of such areas are unlikely to provide habitat to many species, and as such could suggest higher levels of biologically relevant intact habitat than justified in some regions (e.g. the Sahara).

We calculated three definitions of habitat intactness based on RSR scores: (i) The RSR score described above (hereafter labelled 'nlc'); (ii) The RSR score, but with the constraint that any areas with <50% of the area in wilderness, as defined by the Last of the Wild dataset, version 2 (Wildlife Conservation Society, Center for International Earth Science Information Network, 2005), are set to 0 (hereafter 'ltw'); and (iii) The RSR score, but with the constraint that any areas with <50% of the area in International Union for Conservation of Nature (IUCN) protected areas classes I to IV (Dudley, 2010) are set to 0 (hereafter 'wpa'). We used the August 2013 version of the IUCN World Database on Protected Areas (WDPA) for this analysis (IUCN & UNEP-WCMC, 2013). All RSR scores were calculated in R 3.0 (R Development Core Team, 2013).

To match the biome vulnerability data, we produced RSR surfaces at a 48 km spatial resolution for the two spatial scales and three definitions of habitat intactness. For the medium-scale analyses, this involved calculating the mean RSR scores of all 100 4.8 × 4.8 km pixels within each 48 × 48 km pixel. We calculated a measure of species-area weighted habitat loss (L) = 1 – RSR and classified L into five classes that align with the biome shift vulnerability classes (Gonzalez *et al.*, 2010) – very low habitat loss ($L < 0.05$), low ($0.05 \leq L < 0.2$), medium ($0.2 \leq L < 0.8$), high ($0.8 \leq L < 0.95$), and very high ($L \geq 0.95$) – for each of the six analyses (Figures S1–S3; Table S1).

Spatial analysis of biome shifts due to climate change

We used spatial data of the vulnerability of ecosystems to biome shifts from an analysis of University of East Anglia Climate Research Unit 1901–2002 historical climate trends and MC1 DGVM 1990–2100 vegetation projections for three Intergovernmental Panel on Climate Change (IPCC) emissions scenarios (B1, A1B, A2) and three general circulation models (CSIRO Mk3, HadCM3, MIROC 3.2 medres) (Gonzalez *et al.*, 2010). Vulnerability is a function of three components: exposure, sensitivity, and adaptive capacity (Intergovernmental Panel on Climate Change, 2007). Certain biomes will inherently exhibit a higher sensitivity, and therefore higher vulnerability, to climate change than other biomes. The MC1 DGVM quantifies this sensitivity through process-based modelling of biogeography, biogeochemistry, and wildfire. The vulnerability of ecosystems to biome shifts (V) is the confidence level (Intergovernmental Panel on Climate Change, 2007, 2013) that the potential vegetation biome of a pixel may change between 1990 and 2100. Vulnerability varies on a scale of confidence values ranging from 0 to 1 to follow Intergovernmental Panel on Climate Change (2007) methods to characterize uncertainty. We used the same thresholds for the biome shift vulnerability classes and the habitat intactness classes: very low vulnerability ($V < 0.05$), low ($0.05 \leq V < 0.2$), medium

($0.2 \leq V < 0.8$), high ($0.8 \leq V < 0.95$), and very high ($V \geq 0.95$). We aligned the biome shift vulnerability data to the exact extent of the habitat intactness results, masking out GlobCover bare, snow, and ice areas (Table S2).

Combination of relative species richness and climate change-induced biome shifts

For each of the six analyses of habitat intactness (measured by RSR) outlined above, we determined the overlap of the habitat loss factor (L) and the biome shift vulnerability classes (V) by classifying pixels where both L and V fell within the same range. To avoid under- or overestimation of the vulnerability of certain areas of very high or very low L or V, we included two exceptional combinations of medium vulnerability (very high L and medium V, very high V and medium L) in the high class and two (very low L and medium V, very low V and medium L) in the low class, the same method used by Gonzalez *et al.* (2010). We considered refugia to be any areas that had a combined classification of very low or low, consistent with Groves *et al.* (2012). In addition, we calculated vulnerability by biome using the vegetation biomes modelled by the MC1 DGVM for a standard baseline 1961–1990 climate (Gonzalez *et al.*, 2010).

All original data were unprojected rasters in the geographical reference system, where the surface area of pixels varied with latitude. The data cover the terrestrial vegetated area of the world, except Antarctica. We excluded bare areas, snow, and ice from the analyses because our goal was to identify refugia for vegetation biomes. We also excluded areas that were less than 50% land at the 48×48 km scale.

To accurately calculate land areas, we divided global files into six continental files and projected each continent to Lambert Azimuthal Equal-Area projection (Gonzalez *et al.*, 2010). We conducted all spatial analyses on the equal-area projection data at 48×48 km spatial resolution. We calculated global totals and averages by combining the continental results, weighted by the area of each continent. As a case study, we also conducted spatial analyses for the US National Park System, which consists of 401 units that cover 340 000 km². Spatial analyses were conducted in ArcGIS 10.1 (Esri, Redlands, California), and ENVI 5.0.3/IDL 8.2.3 (Exelis, Boulder, CO, USA).

Results

Our results show that three-quarters of global terrestrial vegetated area is vulnerable to climate change resulting from high vulnerability to biome shifts and low levels of habitat intactness. However, the spatial extent of such areas and of refugia to future impacts of climate change is dependent on the definition of habitat intactness and on the spatial scale of the analyses of habitat intactness. Globally, 28% of terrestrial vegetated area can be considered refugia if all natural vegetated land cover (nlc) is considered (Table 1; Fig. 1). This, however, drops to 17% if only areas that are at least

50% wilderness (ltw) at a scale of 48×48 km are considered and to 10% at a scale of 4.8×4.8 km (Table 1; Fig. 2). Only 2% of vegetated area globally is classified as refugia when considering areas at least 50% protected by the global protected area network (wpa) at the 48×48 km scale; this drops to 1% at the 4.8×4.8 km scale (Table 1; Fig. 3).

While up to three-quarters of global terrestrial vegetated area is highly to very highly vulnerable to the combined effects of low habitat intactness and biome shifts (Table 1), the spatial extent of refugia varies considerably among continents. Europe has the lowest fraction of its area in refugia of all continents, followed by Asia (Table 1; Fig. 1). By contrast, over half of the area of Australia and approximately a third of the vegetated area of South America and Africa are classified as refugia, based on the 'nlc' definition of intactness (Table 1; Fig. 1). South and Northeast Asia have the most extensive areas of high vulnerability (Fig. 1), but Europe also has few areas with low or very low vulnerability (refugia), as do large sections of North America (Fig. 1). Again, refugia are consistently less widespread when only wilderness is considered, and much less widespread when only protected areas are considered.

The spatial scale of the analyses also affected our findings. For the wilderness and protected areas measures of intactness, refugia, and areas of high and low vulnerability are more widespread at the coarse than the medium spatial scale. By contrast, for the natural land cover measure of intactness, spatial scale did not affect the results when considering both vulnerability to biomes shifts and habitat intactness (Table 1).

Our results also reveal extensive variation in the extent of refugia and areas of high and very high vulnerability among different biomes. As a fraction of biome area, deserts, tropical evergreen broadleaf forest, and tundra and alpine have the greatest fraction of area in potential refugia at the medium scale for the three definitions of intactness (Fig. 4, Table S3). By total surface area, tropical evergreen broadleaf forest has the greatest area in potential refugia at both spatial scales and all definitions of intactness (Table S4). The deserts and tropical evergreen broadleaf forests of central Australia and the western Amazon, respectively, encompass the most extensive refugia globally. In contrast, a maximum of 6% of temperate mixed forests are in potential refugia, while other temperate forests and tropical woodlands are also poorly represented in potential refugia (Fig. 4, Table S3). Again, the definition of habitat intactness had a considerable impact on this finding. For example, wilderness-dominated refugia cover only a small fraction of temperate shrubland (1% of biome area at the medium scale), though nonwilderness

Table 1 Vulnerability to biome shifts due to climate change, as mediated by habitat intactness, fraction (%) of terrestrial vegetated area

Scale	Intactness	Area	Very low	Low	Medium	High	Very high
4.8 km	nlc	World	<0.5	28	69	2	0
		Africa	<0.5	31	68	1	0
		Asia	<0.5	19	74	7	0
		Australia	0	53	46	1	0
		Europe	0	4	95	1	0
		North America	<0.5	32	68	<0.5	0
		South America	<0.5	38	61	1	0
4.8 km	ltw	World	<0.5	10	53	36	1
		Africa	0	3	53	43	1
		Asia	0	7	51	41	1
		Australia	0	24	68	8	<0.5
		Europe	0	1	29	70	<0.5
		North America	0	11	65	23	<0.5
		South America	<0.5	18	47	35	1
4.8 km	wpa	World	<0.5	1	35	64	1
		Africa	0	1	38	60	1
		Asia	<0.5	<0.5	28	70	1
		Australia	0	1	57	42	<0.5
		Europe	0	0	24	76	<0.5
		North America	0	1	35	64	<0.5
		South America	<0.5	3	35	62	<0.5
48 km	nlc	World	<0.5	28	68	4	0
		Africa	<0.5	30	69	1	0
		Asia	0	19	70	10	0
		Australia	0	53	44	2	0
		Europe	0	4	94	2	0
		North America	<0.5	29	71	<0.5	0
		South America	1	36	62	1	0
48 km	ltw	World	<0.5	17	35	47	1
		Africa	0	10	35	54	1
		Asia	0	13	36	50	1
		Australia	0	41	43	15	<0.5
		Europe	0	2	18	80	<0.5
		North America	<0.5	18	45	37	<0.5
		South America	<0.5	27	23	49	1
48 km	wpa	World	<0.5	2	25	72	1
		Africa	0	2	32	65	1
		Asia	<0.5	1	20	78	1
		Australia	0	3	47	50	<0.5
		Europe	0	<0.5	9	90	<0.5
		North America	0	3	25	72	<0.5
		South America	<0.5	4	22	74	1

refugia of this biome type remain relatively widespread (22% of biome area). By contrast, wilderness-dominated refugia of boreal forests remain fairly widespread, and cover over half of the roughly 25% of the area of this biome classified as refugia.

For the US National Park System, the wilderness (ltw) analyses indicate that up to one half of system area is in potential refugia while up to one quarter is in areas of high to very high vulnerability (Table S6).

Refugia are mainly in Alaska and remote parts of the interior western United States (Figure S4). Boreal conifer forest has the highest fraction of biome area in potential refugia (48 ltw) while the tropical woodland and temperate mixed forest biomes are most vulnerable (Table S7). In terms of absolute area, the tundra and alpine biome has the most extensive refugia while temperate shrubland is most vulnerable (Table S8).

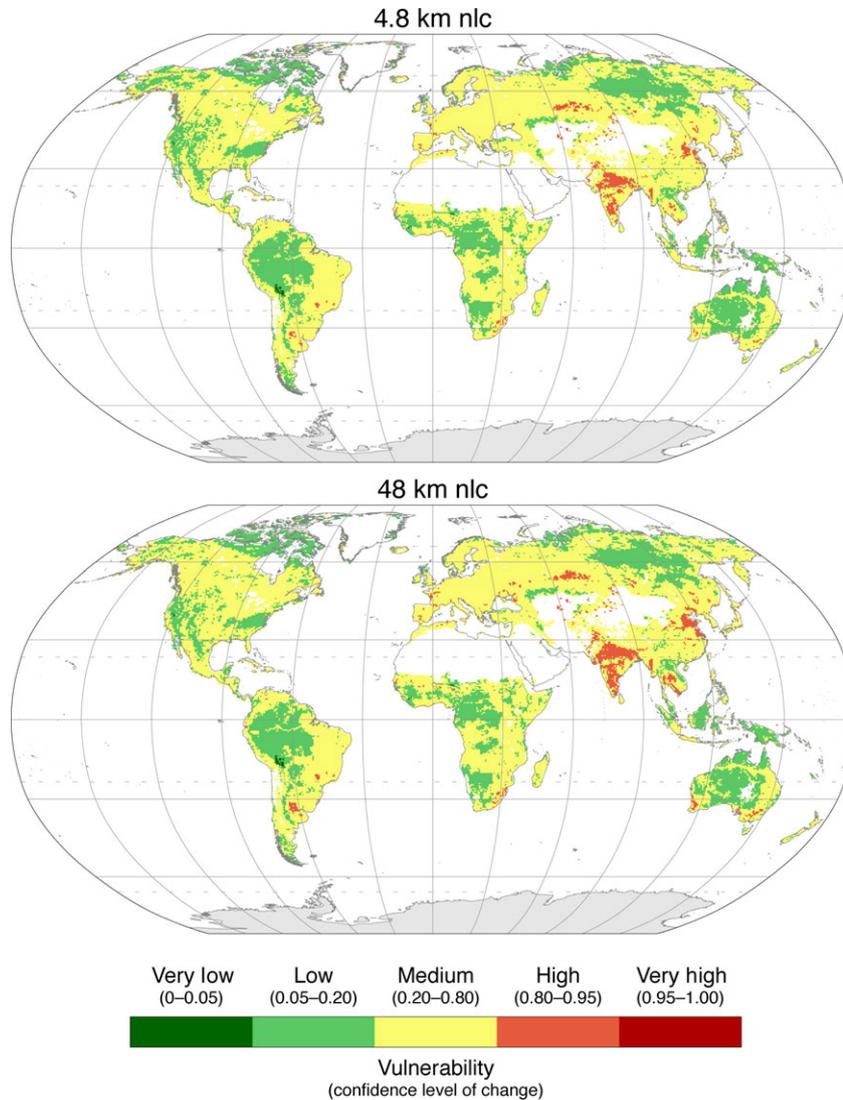


Fig. 1 Vulnerability to biome shifts due to climate change at the 4.8×4.8 km and 48×48 km spatial scales, as mediated by habitat intactness, with intact habitat defined as all natural vegetated GlobCover land classes (nlc). Areas shown in white are those without vegetation (bare ground, snow, and ice).

Discussion

Our results add to the growing evidence (Jetz *et al.*, 2007; Lee & Jetz, 2008; Gonzalez *et al.*, 2010; Watson *et al.*, 2013) that the combination of low habitat intactness and vulnerability to climate change threatens biodiversity in many of the globe's terrestrial ecosystems. They are the first to show that the definition and scale of intactness has a major impact on the projected extent of vulnerability. Our results have considerable conservation implications, as habitat intactness gives a measure of the adaptive capacity of species and therefore can comprise an important component of the relative vulnerability to climate change in different regions (Watson *et al.*, 2013).

While the value of quantifying habitat intactness for the identification of spatial priorities for climate change conservation is undisputed, identifying what constitutes sufficiently intact habitat is less straightforward. First, the spatial scale of the analysis and the natural land cover types that are considered as habitat are important, because what constitutes sufficient habitat is a species-specific concept (Wiens, 1989). For example, a region that contains forest blocks of up to 10 ha in size may offer sufficiently intact habitat for most forest beetles in the region. The extent of forest cover, however, is not a good measure of habitat intactness for grassland species that inhabit the same region, nor are ~10 ha forest fragments sufficient for large, forest-dependent top predators. Second, context matters in the sense that a

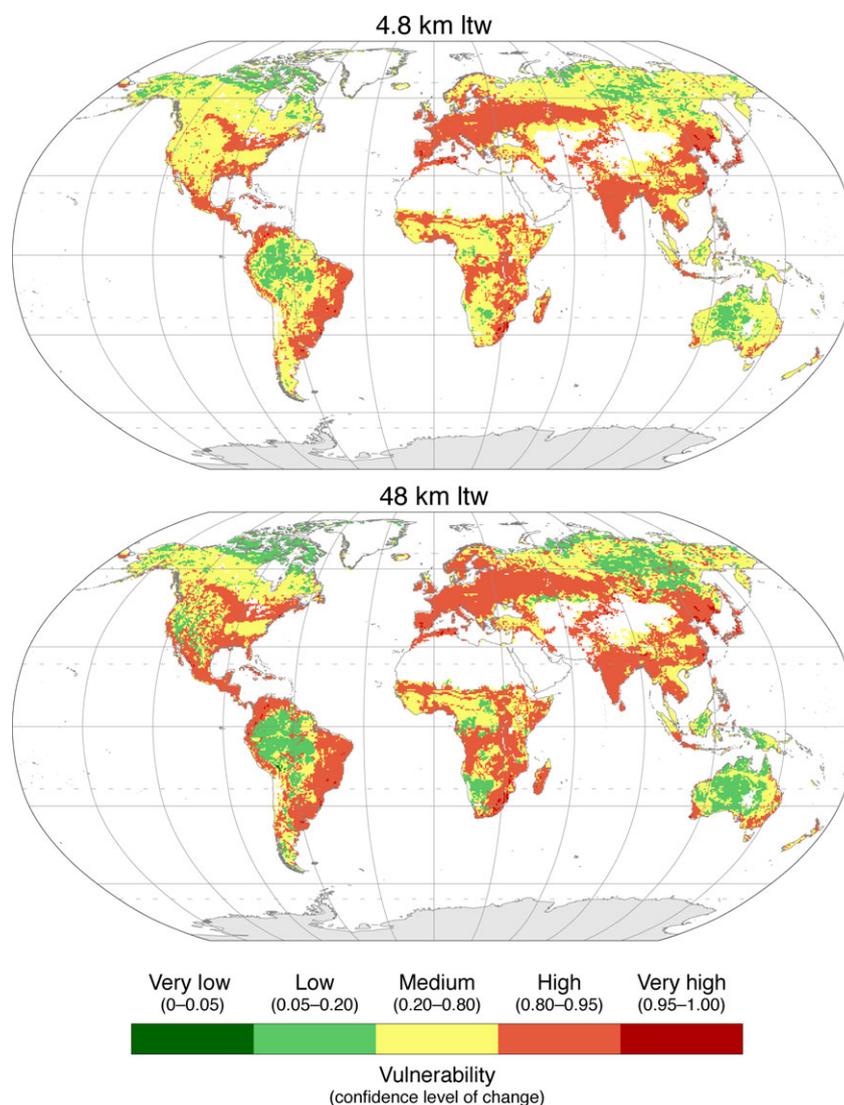


Fig. 2 Vulnerability to biome shifts due to climate change at the 4.8×4.8 km and 48×48 km spatial scales, as mediated by habitat intactness, with intact habitat defined as all natural vegetated GlobCover land classes with $\geq 50\%$ of the area in wilderness (Itw). Areas shown in white are those without vegetation (bare ground, snow, and ice).

region with extensive natural habitat but high levels of human activity (i.e. urbanization) in the nonhabitat (matrix) parts of the region is likely to have less biodiversity (Kupfer *et al.*, 2006; Koh & Ghazoul, 2010) and lower adaptive capacity (Gillson *et al.*, 2013) than a region with similar amounts of natural habitat but a more benign matrix (i.e. agroforestry). Finally, our results suggest that regions with high levels of habitat intactness and extensive protected areas are more resilient to biome shifts due to climate change than regions with similar levels of intactness but without protected area status (Gillson *et al.*, 2013). Nevertheless, we recognize that protected area status has not seemed to mitigate some impacts of climate change occurring across extensive areas, such as increased wildfire or forest

dieback. Furthermore, the high level of vulnerability under the analyses that used the protected area definition of intactness (wpa) suggests that the current configuration of the world protected areas system may be insufficient to guard against the combined effects of climate change and habitat fragmentation.

An additional issue is whether to only measure habitat extent or whether the configuration of the habitat (habitat fragmentation) also needs to be considered. For most species, habitat extent is much more important than configuration (Fahrig, 2003), but again the relative effects of extent and configuration are species-specific. The species-focused nature of most studies examining the combined effects of habitat intactness and climate vulnerability is the most likely reason for a lack of other

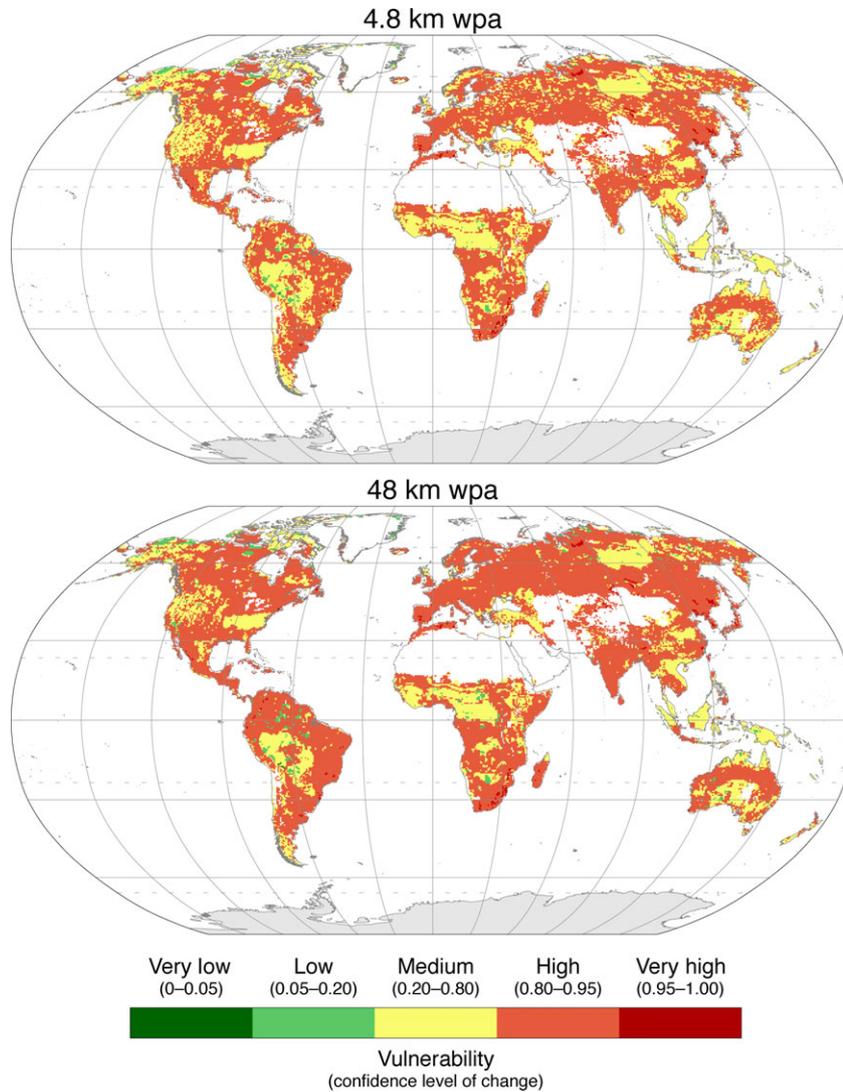


Fig. 3 Vulnerability to biome shifts due to climate change at the 4.8×4.8 km and 48×48 km spatial scales, as mediated by habitat intactness, with intact habitat defined as all natural vegetated GlobCover land classes with $\geq 50\%$ of the area in protected areas (wpa). Areas shown in white are those without vegetation (bare ground, snow, and ice).

work considering different metrics of intactness, as the measures of intactness chosen are simply the ones most appropriate for the species considered. As Watson *et al.* (2013) point out, however, ecosystem-based assessments of vulnerability to climate change provide an important complement to such species-based analyses. Our results show that, for ecosystem-focused analyses, how intactness is measured has a major impact on results.

Indeed, the degree to which our findings support previous studies depends on the definition of habitat intactness. Our results are broadly similar to those of Watson *et al.* (2013) when we use natural land cover alone to calculate our RSR scores (nlc). We both identify the most vulnerable areas globally to be the Indian subcontinent, southeast China, and parts of South

America, Australia, and central Europe, though Watson *et al.* (2013) show larger areas of vulnerability in North America and Europe. The broad similarity in these results is not surprising since Watson *et al.* (2013) use extent of natural land cover per ecoregion as an indicator of habitat intactness. Our results, however, show larger refugia in parts of Siberia and northern North America, perhaps because our analyses used both historical and projected climate, while Watson *et al.* (2013) only used projected climate. If we use the wilderness (ltw) definition of habitat intactness, our results additionally highlight the near-complete lack of refugia in Europe, Central America and Southeast Asia (outside of Indonesia), while the protected areas (wpa) definition of intactness highlights the near-complete lack of protected refugia. Indeed, one of the more

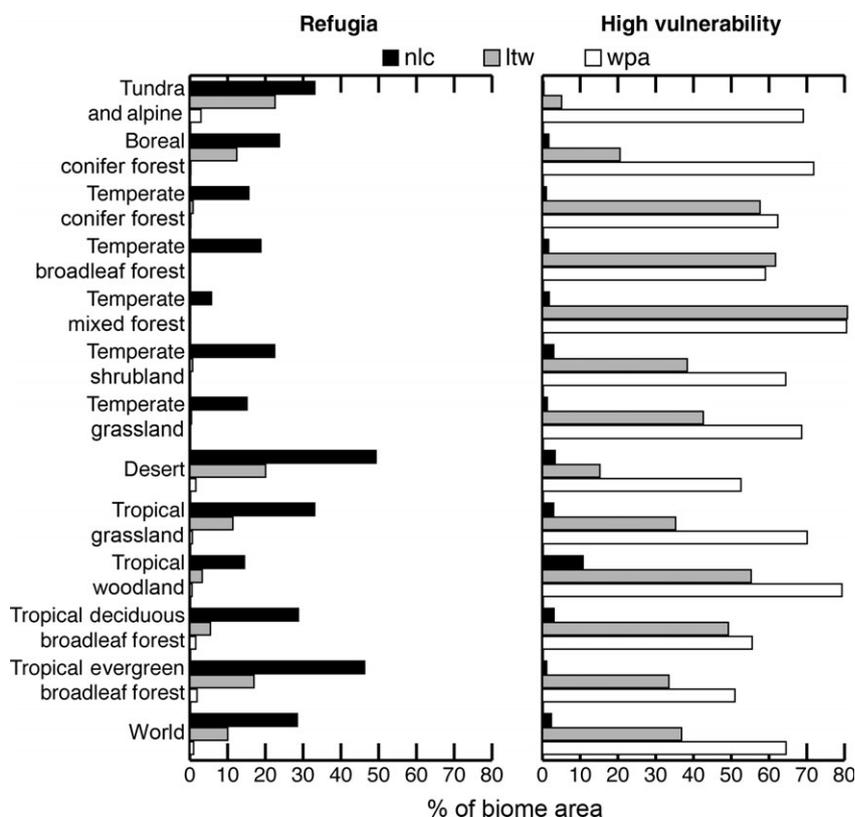


Fig. 4 Refugia and high vulnerability areas by biome at the 4.8 km \times 4.8 km scale for three measures of habitat intactness (nlc, ltw, wpa), as a fraction of biome area. Biomes are listed in the order of predominant location from the Poles to the Equator.

sobering results that emerges from our analyses is quantitative support for assertions (e.g. Hannah *et al.*, 2007) that the current protected area system is wholly inadequate to protect ecosystems in the face of climate change, as refugia that fall at least 50% within protected areas cover a maximum of 2% of the vegetated areas of the Earth. As the strictly protected areas, we consider here (IUCN categories I – IV) cover 6% of the global terrestrial area (Jenkins & Joppa, 2009), this means that only 17% (medium scale) or 34% (coarse scale) of protected areas are also refugia.

Our analyses also generally support work based on climatic stability alone (e.g. Iwamura *et al.*, 2010). They highlight that, despite ongoing deforestation, tropical rainforests show relatively low vulnerability to shifts at the biome level and contain extensive areas of potential refugia (Malhi *et al.*, 2008), although vulnerability may be higher at the species level (Reu *et al.*, 2011). The intactness of upper Amazonian forests leads our analyses to place higher value on these areas than climate-only analyses. Our results also highlight that, despite the relatively low climatic stability of boreal forests (Gonzalez *et al.*, 2010; Watson *et al.*, 2013), the intactness and wildness of this biome allow it to contain fairly extensive climate refugia compared to temperate forests,

which are highly vulnerable due to low habitat intactness and relatively low climatic stability.

The relatively large differences in results between the medium and coarse-scale analyses indicate that medium-scale pixels with high (and low) natural land cover frequently cluster within coarse-scale pixels. For example, most coarse-scale pixels (48 \times 48 km) with less than 50% wilderness will tend to have some medium-scale (4.8 \times 4.8 km) pixels within them with over 50% wilderness. The converse is also true; coarse-scale pixels with over 50% wilderness tend also to include medium-scale pixels below this threshold. As a result, any of our analyses that involved thresholds (50% wilderness or protected area) tended to have more extreme values (high or low vulnerability) at coarse scales; medium-scale analyses gave more intermediate vulnerability scores due to the averaging of the relative richness scores. These results are unsurprising in that it is well-established that larger pixel sizes (coarse grain analyses) can lead to reductions in perceived deforestation (e.g. Nepstad *et al.*, 1999), but they nonetheless have important conservation implications. For example, the medium-scale analyses are important as some areas identified as having high vulnerability to climate change at coarse scales in the wilderness analysis have only moderate vulnerability at

medium scales. This indicates that some wilderness-dominated 4.8×4.8 km pixels exist and therefore have considerable conservation value for species with smaller habitat requirements. As such mismatches between scales are frequently located in relatively human-dominated regions (e.g. parts of the conterminous United States and Scandinavia in the wilderness analyses) with no remaining large wilderness areas, these medium-scale areas of moderate vulnerability may be of considerable importance as they may represent the areas of the highest conservation value in such regions. Simply running the analyses at medium scales, however, can also be misleading because many areas have low vulnerability at coarse scales (i.e. they are climate refugia) but moderate vulnerability at medium scales. Such areas have considerable conservation value for most species but are characterized by pockets of high anthropogenic activity. It is important to note that changing pixel sizes would quantitatively change our findings, but not the main conclusion – that the perceived habitat intactness of any given region can depend on the spatial scale of the analysis. Changing the thresholds in our analyses (i.e. to 75% wilderness) would also have a minor quantitative effect on our findings (Table S5), but again would not affect our main conclusion.

Our study has a number of limitations with management implications. The first set of these relate to the scale at which our results are useful for managers. Our results are limited by the quality of the land cover data [the associated uncertainty in classification accuracy for land cover varies 68–74% (Defourny *et al.*, 2010)], class aggregation to the biome level, and the quality and resolution of the biome shift data [discussed further in Gonzalez *et al.* (2010)]. Moreover, the GlobCover land cover class definitions do not provide any direct information on land use. For example, a broad-leaf class might contain natural and/or managed forest, creating spatial variation in habitat quality within a single class. In addition, by focusing on the dominant natural land cover type in each pixel, due to the overwhelming importance of habitat extent on biodiversity (Fahrig, 2003), we may undervalue regions with high natural habitat heterogeneity. Areas of high habitat heterogeneity have been shown to promote population stability, albeit at a much finer spatial scale (Oliver *et al.*, 2010). As such, our results are intended to inform broad-scale landscape conservation planning, rather than fine-scale local efforts.

Similarly, our results are affected by the limitations of the Last of the Wild and WPA datasets. A major limitation of the Last of the Wild – already highlighted by Sanderson *et al.* (2002) – is the age of the underlying datasets. Even the updated version (published 2005) that we use here is based on data collected between 1999 and

2004 (Wildlife Conservation Society, Center for International Earth Science Information Network, 2005). This means that, in some rapidly urbanizing areas (e.g. Southeast Asia), the extent of refugia may be considerably less than our results suggest. The main issues with the WPA are those of omissions – e.g. parks for which vector boundary data is missing and considerable variability in the *de facto* protection provided by the protected areas. The former is likely a relatively minor issue for the global and continental-scale analyses we conduct here (Jenkins & Joppa, 2009) but the latter is potentially important in many areas (e.g. Leroux *et al.*, 2010). That said, evidence strongly indicates that, on the whole, the global protected area network – as mapped by the WPA – reduces natural land cover conversion (Joppa & Pfaff, 2011).

A second limitation results from our focus on biomes, rather than species. Use of the biome as a unit of analysis may understate vulnerability because it allows for some changes in species composition without conversion into a different biome. We do not examine how the distributions of the refugia that we identify overlap with global patterns of biodiversity or with global, largely species-driven conservation prioritization schemes [e.g. hotspots (Myers *et al.*, 2000)]. Our results are therefore of themselves insufficient for prioritization of specific taxa and not intended as such. Instead, our species-neutral but theoretically grounded measure of intactness (relative species richness) offers an important complement to species-focused analyses and conservation approaches. This is because an ecosystems approach avoids a number of issues arising from species-related conservation. For one, we avoid the issue of taxonomic bias, which can, for example, affect conservation network design (Grand *et al.*, 2007) and spatial conservation prioritization efforts (Grantham *et al.*, 2010; Saetersdal & Gjerde, 2011). We also avoid the problem of assessing the conservation value of under-surveyed areas; a recent study shows that highly intact tropical forests are likely to contain both larger numbers and proportionately more undiscovered species than less intact areas (Giam *et al.*, 2012). Finally, taxon-specific analyses of climate vulnerability can miss potentially very important impacts of interactions between species (Van der Putten *et al.*, 2010).

A third limitation is that our analyses of habitat intactness are based on current land cover and do not use future projections, which may reveal even more substantial vulnerability of ecosystems to habitat loss (e.g. Lee & Jetz, 2008). Again, our analyses are intended to complement such studies and encourage proactive conservation measures, as reduction in nonclimate change related threats is an important climate change adaptation strategy (Morecroft *et al.*, 2012) and maintaining high levels of existing natural habitat is a particular priority (Hodgson *et al.*, 2009). Finally, more study is required to integrate

our results into global and broad-scale conservation planning efforts since our analyses contain no information on returns on investment (e.g. Iwamura *et al.*, 2010) or considerations of other social goals such as maintaining ecosystem services (e.g. Venter *et al.*, 2009).

While the spatial resolution of the present analysis is too coarse for use in small areas, the results can be useful for broad landscapes. The US National Park Service, which manages an extensive system of protected areas across North America, considers the vulnerability of ecosystems to biome shifts as one potential factor for the prioritization, across the system, of natural resource management adaptation measures, such as strict conservation of refugia and prescribed burning of vulnerable areas (Gonzalez, 2011). Similarly, the US Fish and Wildlife Service considers vulnerability to biome shifts in managing its separate system of wildlife refuges (Griffith *et al.*, 2009). Our results indicate substantial vulnerability of the US National Park System to biome shifts and habitat loss.

In conclusion, our research adds to the few efforts that have analysed the vulnerability of ecosystems to both climate change and habitat intactness globally and illustrates that how habitat intactness is measured has a major impact on such analyses. We identify the locations of potential refugia and vulnerable areas, spatial information potentially useful for the adaptation of natural resource management planning at a broad scale. Our spatial results (data files available from the corresponding author) can help resource managers more effectively develop adaptation measures, including the identification of refugia for strict conservation and potential corridors to facilitate dispersal as vegetation and wildlife ranges shift. Despite the magnitude of the challenges of habitat loss and climate change, refugia may continue to provide hope for the conservation of wild species.

Acknowledgements

Many thanks to Emma Brooks and Simon Willcock for their comments on this manuscript. This study was supported by an Adventures in Research Grant from the University of Southampton to FE and JD and by Climate Change Response Program funding from the US National Park Service to PG. We are grateful to Björn Reu and an anonymous reviewer for their constructive comments to improve the quality of the manuscript.

References

- Alagador D, Cerdeira JO, Araújo MB (2014) Shifting protected areas: scheduling spatial priorities under climate change. *Journal of Applied Ecology*, **51**, 703–713.
- Arrhenius O (1921) Species and area. *Journal of Ecology*, **9**, 95–99.
- Baron JS, Gunderson L, Allen CD *et al.* (2009) Options for national parks and reserves for adapting to climate change. *Environmental Management*, **44**, 1033–1042.
- Boakes EH, Mace GM, McGowan PJK, Fuller RA (2010) Extreme contagion in global habitat clearance. *Proceedings of the Royal Society B-Biological Sciences*, **277**, 1081–1085.
- Bontemps S, Defourny P, Van Bogaert E, Arino O, Kalogirou V, Perez JR (2011) GlobCover 2009 – Products description and validation report. Louvain.
- Brook BW, Sodhi NS, Bradshaw CJ (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453–460.
- Brooks TM, Pimm SL, Collar NJ (1997) Deforestation predicts the number of threatened birds in insular southeast Asia. *Conservation Biology*, **11**, 382–394.
- Butchart SHM, Walpole M, Collen B *et al.* (2010) Global biodiversity: indicators of recent declines. *Science*, **328**, 1164–1168.
- Cabral JS, Jeltsch F, Thuiller W *et al.* (2013) Impacts of past habitat loss and future climate change on the range dynamics of South African Proteaceae. *Diversity and Distributions*, **19**, 363–376.
- Carvalho SB, Brito JC, Crespo EJ, Possingham HP (2010) From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. *Global Change Biology*, **16**, 3257–3270.
- Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, **16**, 488–502.
- Defourny P, Bontemps S, Obsomer V *et al.* (2010) Accuracy assessment of global land cover maps: lessons learnt from the GlobCover and GlobCorine experiences. In: *Proceedings of the ESA Living Planet Symposium Bergen*. (ed. Lacoste-Francis H), ESA Communications, Noordwijk, the Netherlands.
- Dudley N (ed.) (2010) *Guidelines for Applying Protected Area Management Categories*. International Union for Conservation of Nature, Gland, Switzerland.
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.
- Findlay CS, Houlihan J (1997) Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology*, **11**, 1000–1009.
- Foden WB, Butchart SHM, Stuart SN *et al.* (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE*, **8**, e65427.
- Giam X, Scheffers BR, Sodhi NS, Wilcove DS, Ceballos G, Ehrlich PR (2012) Reservoirs of richness: least disturbed tropical forests are centres of undescribed species diversity. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 67–76.
- Gillson L, Dawson TP, Jack S, McGeoch MA (2013) Accommodating climate change contingencies in conservation strategy. *Trends in Ecology & Evolution*, **28**, 135–142.
- Gonzalez P (2011) Science for natural resource management under climate change. *Issues in Science and Technology*, **27**, 65–74.
- Gonzalez P, Neilson RP, Lenihan JM, Drapek RJ (2010) Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. *Global Ecology and Biogeography*, **19**, 755–768.
- Grand J, Cummings MP, Rebelo TG, Ricketts TH, Neel MC (2007) Biased data reduce efficiency and effectiveness of conservation reserve networks. *Ecology Letters*, **10**, 364–374.
- Grantham HS, Pressey RL, Wells JA, Beattie AJ (2010) Effectiveness of biodiversity surrogates for conservation planning: different measures of effectiveness generate a kaleidoscope of variation. *PLoS ONE*, **5**, e11430.
- Griffith B, Scott JM, Adamcik R *et al.* (2009) Climate change adaptation for the US National Wildlife Refuge System. *Environmental Management*, **44**, 1043–1052.
- Groves CR, Game ET, Anderson MG *et al.* (2012) Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation*, **21**, 1651–1671.
- Hannah L, Midgley G, Anelman S *et al.* (2007) Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, **5**, 131–138.
- Hanski I, Zurita GA, Bellocq MI, Rybicki J (2013) Species-fragmented area relationship. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 12715–12720.
- He F, Hubbell SP (2011) Species-area relationships always overestimate extinction rates from habitat loss. *Nature*, **473**, 368–371.
- Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009) Climate change, connectivity and conservation decision making: back to basics. *Journal of Applied Ecology*, **46**, 964–969.
- Intergovernmental Panel on Climate Change (2007) *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, Cambridge.
- Intergovernmental Panel on Climate Change (2013) *Climate Change 2013: The Physical Science Basis*. Cambridge University Press, Cambridge.
- IUCN and UNEP-WCMC (2013) The World Database on Protected Areas (WDPA). Cambridge, UNEP-WCMC. Available at: www.protectedplanet.net (accessed September 10 2013).
- Iwamura T, Wilson KA, Venter O, Possingham HP (2010) A climatic stability approach to prioritizing global conservation investments. *PLoS ONE*, **5**, e15103.
- Jenkins NJ, Joppa L (2009) Expansion of the global protected area system. *Biological Conservation*, **142**, 2166–2174.

- Jetz W, Wilcove DS, Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5**, e157.
- Joppa LN, Pfaff A (2011) Global protected area impacts. *Proceedings of the Royal Society B*, **278**, 1633–1638.
- Keppel G, Van Niel KP, Wardell-Johnson GW *et al.* (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, **21**, 393–404.
- Klausmeyer KR, Shaw MR, MacKenzie JB, Cameron DR (2011) Landscape-scale indicators of biodiversity's vulnerability to climate change. *Ecosphere*, **2**, art88.
- Koh LP, Ghazoul J (2010) A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. *Conservation Biology*, **24**, 994–1001.
- Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, **15**, 8–20.
- Lee TM, Jetz W (2008) Future battlegrounds for conservation under global change. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 1261–1270.
- Leroux SJ, Krawchuk MA, Schmiegelow F, Cumming SG, Lisgo K, Anderson LG, Petkova M (2010) Global protected areas and IUCN designations: Do the categories match the conditions? *Biological Conservation*, **143**, 609–616.
- Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li W, Nobre CA (2008) Climate change, deforestation, and the fate of the Amazon. *Science*, **319**, 169–172.
- Mantyka-Pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239–1252.
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Biodiversity Synthesis*. World Resources Institute, Washington DC.
- Morecroft MD, Crick HQP, Duffield SJ, Macgregor NA (2012) Resilience to climate change: translating principles into practice. *Journal of Applied Ecology*, **49**, 547–551.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Nepstad DC, Verssimo A, Alencar A *et al.* (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.
- Oliver T, Roy DB, Hill JK, Brereton T, Thomas CD (2010) Heterogeneous landscapes promote population stability. *Ecology Letters*, **13**, 473–484.
- Oliver TH, Smithers RJ, Bailey S, Walmsley CA, Watts K (2012) A decision framework for considering climate change adaptation in biodiversity conservation planning. *Journal of Applied Ecology*, **49**, 1247–1255.
- Pereira HM, Leadley PW, Proença V *et al.* (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496–1501.
- Pimm SL, Raven P (2000) Extinction by numbers. *Nature*, **403**, 843–845.
- Ponce-Reyes R, Nicholson E, Baxter PWJ, Fuller RA, Possingham H (2013) Extinction risk in cloud forest fragments under climate change and habitat loss. *Diversity and Distributions*, **19**, 518–529.
- R Development Core Team (2013) R: A language and environment for statistical computing.
- Reu B, Zaehle S, Proulx R, Bohn K, Kleidon A, Pavlick R, Schmittlein S (2011) The role of plant functional trade-offs for biodiversity changes and biome shifts under scenarios of global climatic change. *Biogeosciences*, **8**, 1255–1266.
- Reu B, Zaehle S, Bohn K, Pavlick R, Schmittlein S, Williams JW, Kleidon A (2014) Future no-analogue vegetation produced by no-analogue combinations of temperature and insolation. *Global Ecology and Biogeography*, **23**, 156–167.
- Riordan EC, Rundel PW (2014) Land use compounds habitat losses under projected climate change in a threatened California ecosystem. *PLoS ONE*, **9**, e86487.
- Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Saetersdal M, Gjerde I (2011) Prioritising conservation areas using species surrogate measures: consistent with ecological theory? *Journal of Applied Ecology*, **48**, 1236–1240.
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891.
- Scholze M, Knorr W, Arnell NW, Prentice IC (2006) A climate-change risk analysis for world ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 13116–13120.
- Sólymos P, Lele SR (2012) Global pattern and local variation in species-area relationships. *Global Ecology and Biogeography*, **21**, 109–120.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **365**, 2025–2034.
- Venter O, Laurance WF, Iwamura T, Wilson KA, Fuller RA, Possingham HP (2009) Harnessing carbon payments to protect biodiversity. *Science*, **326**, 1368.
- Visconti P, Pressey RL, Giorgini D *et al.* (2011) Future hotspots of terrestrial mammal loss. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, **366**, 2693–2702.
- Watson JEM, Iwamura T, Butt N (2013) Mapping vulnerability and conservation adaptation strategies under climate change. *Nature Climate Change*, **3**, 989–994.
- Whittaker RJ, Araújo MB, Jepson P, Ladle RJ, Watson JEM, Willis KJ (2005) Conservation Biogeography: assessment and prospect. *Diversity and Distributions*, **11**, 3–23.
- Wiens JA (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- Wildlife Conservation Society, Center for International Earth Science Information Network (2005) Last of the wild project, version 2, 2005 (LWP-2): last of the wild dataset (IGHP). Palisades, NY. NASA Socioeconomic Data and Applications Center (SEDAC). Available at: <http://dx.doi.org/10.7927/H4ZC80SS> (accessed 1 August 2013).

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Habitat loss, with intact habitat defined as all natural vegetated GlobCover land classes.

Figure S2. Habitat loss, with intact habitat defined as all natural vegetated GlobCover land classes with $\geq 50\%$ of the area in wilderness.

Figure S3. Habitat loss, with intact habitat defined as all natural vegetated GlobCover land classes with $\geq 50\%$ of the area in protected areas.

Figure S4. Vulnerability to biome shifts across North America due to climate change, as mediated by habitat intactness, at the 48×48 km spatial scale with intact habitat defined as all natural vegetated GlobCover land classes with $\geq 50\%$ of the area in wilderness (ltw). Bare areas, snow, and ice are not masked.

Table S1. Habitat loss, fraction (%) of terrestrial vegetated area.

Table S2. Vulnerability to biome shifts due to climate change (Gonzalez *et al.*, 2010), fraction (%) of terrestrial area. These results exclude the GlobCover classes for bare areas, snow, and ice.

Table S3. Refugia and high vulnerability areas (% of biome area) by biome. Biomes are in the order of predominant location from the Poles to the Equator.

Table S4. Refugia and high vulnerability areas (million km²) by biome. Biomes are in the order of predominant location from the Poles to the Equator.

Table S5. Analysis of the sensitivity of the vulnerability to biome shifts due to climate change, as mediated by habitat intactness, to intactness thresholds, for North America; fraction (%) of terrestrial vegetated area.

Table S6. Vulnerability to biome shifts due to climate change, as mediated by habitat intactness, of the US National Park System; fraction (%) of area.

Table S7. Refugia and high vulnerability areas (% of biome area) of the US National Park System, by biome. Biomes are in the order of predominant location from the North Pole to the Equator.

Table S8. Refugia and high vulnerability areas (1000 km²) of the US National Park System, by biome. Biomes are in the order of predominant location from the North Pole to the Equator. Total area is less than 340 000 km² due to coarse spatial resolution of data.