



Mapping Direct Human Influence on the World's Mountain Areas

Authors: Rodríguez-Rodríguez, David, and Bomhard, Bastian

Source: Mountain Research and Development, 32(2) : 197-202

Published By: International Mountain Society

URL: <https://doi.org/10.1659/MRD-JOURNAL-D-10-00111.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Mapping Direct Human Influence on the World's Mountain Areas

David Rodríguez-Rodríguez^{1*} and Bastian Bomhard²

* Corresponding author: david.rodriguez@csic.es; davidrg@yaho.es

¹ Institute of Economics, Geography and Demography, Spanish National Research Council (IEGD-CSIC), Albasanz, 26-28, 28037 Madrid, Spain

² United Nations Environment Programme World Conservation Monitoring Centre, 219 Huntingdon Road, CB3 0DL, Cambridge, United Kingdom

Open access article: please credit the authors and the full source.



Mountain areas are of great importance to biodiversity conservation. Also, they have long been reputed as the last remnants of virgin, unspoiled

nature. In this paper, we assess the degree of human impact on mountain ecosystems through the Human Influence Index (HII), using it as a proxy to estimate the degree of threat to mountain biodiversity. We also measured how well the least

human-influenced mountain areas are protected ($HII \leq 10$). Our results show that still-large proportions of mountain areas are under low or moderate human influence, as assessed by the HII. However, these results should be considered carefully, because the HII does not include some important human-made influences affecting mountain ecosystems globally, such as climate change. Finally, 34.7% of the mountain area under low human influence ($HII \leq 10$) is currently covered by nationally designated protected areas.

Keywords: Direct human influence; mountains; Human Influence Index (HII); global mapping; protected areas.

Peer-reviewed: March 2012 **Accepted:** April 2012

Introduction

Human influence on ecosystems has been increasing worldwide due to rapid population growth, increasingly resource-consuming life styles, and technological breakthroughs (McNeill 2000; Macchi 2010). This influence has become so important that mankind is now and in the years to come the main global driver of ecological change (Vitousek et al 1997; Sala et al 2000). Human-altered ecosystems made of mosaics of settlements, infrastructures, agricultural, and forest land clearly dominate the terrestrial biosphere, covering more than three quarters of total ice-free land area (Ellis and Ramankutty 2008). Direct and indirect human impacts on ecosystems have resulted in a global biodiversity crisis that threatens the world's species and ecosystems (Pimm et al 1995; Ricketts et al 2005; Butchart et al 2010).

Mountains have long been admired and protected on the grounds of their wild character and landscape beauty. More recently, the idea underlying mountain protection has shifted to safeguarding the wide number of ecological services these areas provide (Kollmair et al 2005). These services include water provision, supply of natural resources, air purification, agricultural diversity, minimization of natural hazards, cultural diversity, leisure, landscape and spiritual values, income sources for local populations, research and early warning systems, and biodiversity (UNEP-WCMC 2002; EEA 2010a, 2010b; Macchi 2010). Mountains are especially important for biodiversity conservation, because they harbor half of the

world's biodiversity hotspots on only about one quarter of the global terrestrial surface (Price and Butt 2000; Kollmair et al 2005; Kohler and Maselli 2009).

Mountain areas are home to about 22% of the world's population (UNEP-WCMC 2002), with 90% of people living in developing countries, mainly in low-density rural settings (Kohler and Maselli 2009; Macchi 2010). Despite their remoteness and low human population density, many mountain ecosystems are strongly affected by global change drivers such as land use change and especially climate change (Kohler and Maselli 2009; EEA 2010b; Macchi 2010). To deal with this challenge, a number of international agreements addressed biodiversity conservation and sustainable development in mountains, including the Programme of Work on Mountain Biodiversity of the Convention on Biological Diversity (CBD 2004), and Chapter 13 of Agenda 21 (UN 1992).

Here, we assessed direct human impact on the world's mountain areas using the Human Influence Index (HII) as a proxy (SEDAC 2005b). We identified, quantified, and mapped the mountain areas most and least affected by direct human disturbance and then measured to what degree the least influenced mountain areas are covered by protected areas, because such areas could be considered cost-effective options for protecting biodiversity and ecosystem services (Sanderson et al 2002). We discuss our findings in the context of our recent analysis of global mountain protection (Rodríguez-Rodríguez et al 2011) and other relevant analyses.

TABLE 1 Mountain classes.

Mountain class	Criteria
1	Elevation > 4500 m
2	Elevation 3500–4500 m
3	Elevation 2500–3500 m
4	Elevation 1500–2500 m and slope $\pm 2^\circ$
5	Elevation 1000–1500 m and slope $\pm 5^\circ$ or local elevation range (7-km radius) > 300 m
6	Elevation 300–1000 m and local elevation range (7-km radius) > 300 m
7	Isolated inner basins and plateaus less than 25 km ² in extent that are surrounded by mountains but do not themselves meet criteria 1–6

Source: UNEP-WCMC 2002.

Material and methods

We overlaid a global mountain map (UNEP-WCMC 2002) with the global map of the HII developed by the Wildlife Conservation Society and the Center for International Earth Science Information Network based on 9 global datasets (SEDAC 2005b). The HII is an index made up of 4 variables representing human disturbance: population density, land transformation, accessibility, and electrical power infrastructure (Sanderson et al 2002). It aims to represent direct human influence over the land surface as a gradient ranging from 0 (wild or untouched) to 72 (totally modified). We used the 1-km²-pixel HII raster map provided by the Socioeconomic Data and Applications Center (SEDAC 2005b) and intersected it with the widely used global mountain map developed by the United Nations Environment Programme—World Conservation Monitoring System (UNEP-WCMC 2002) to assess the degree of direct human influence on mountain areas. The global mountain map includes all areas that meet the mountain criteria defined by the UNEP-WCMC (2002; Table 1). We used the HII instead of the Human Footprint Index (HFI; SEDAC 2005a), because we were interested in a globally comparable measure of the absolute human influence on mountains, not the relative human influence in different biomes and realms measured by the HFI (Sanderson et al 2002; Kier et al 2009).

Sanderson et al (2002) defined the areas scoring $HII \leq 10$ as the least influenced or wildest areas in all biomes. Accordingly, we defined three ranges of human impact on mountains according to the resulting HII score for each cell: low ($HII \leq 10$), moderate ($10 < HII < 25$) and high ($HII \geq 25$). We then overlaid the least influenced mountain areas (ie cells with HII values from 0 to 10) with a global protected areas layer to evaluate the extent of

their protection. For this we used the January 2010 version of the World Database on Protected Areas (WDPA; IUCN and UNEP-WCMC 2010). In line with current best practice, we considered only nationally designated protected areas whose area is reported in the WDPA (Jenkins and Joppa 2009, 2010; Rodríguez-Rodríguez et al 2011). For protected areas recorded only as points in the WDPA, we created a circular buffer around the point equal to the reported area for the protected area, an approach that has been shown to have minor error at coarser scales (Jenkins and Joppa 2009). We then merged the buffered point layer with the polygon layer of the WDPA and dissolved both layers to prevent double counting. All calculations were made with ArcGIS version 9.3 in a Mollweide equal-area projection.

Results

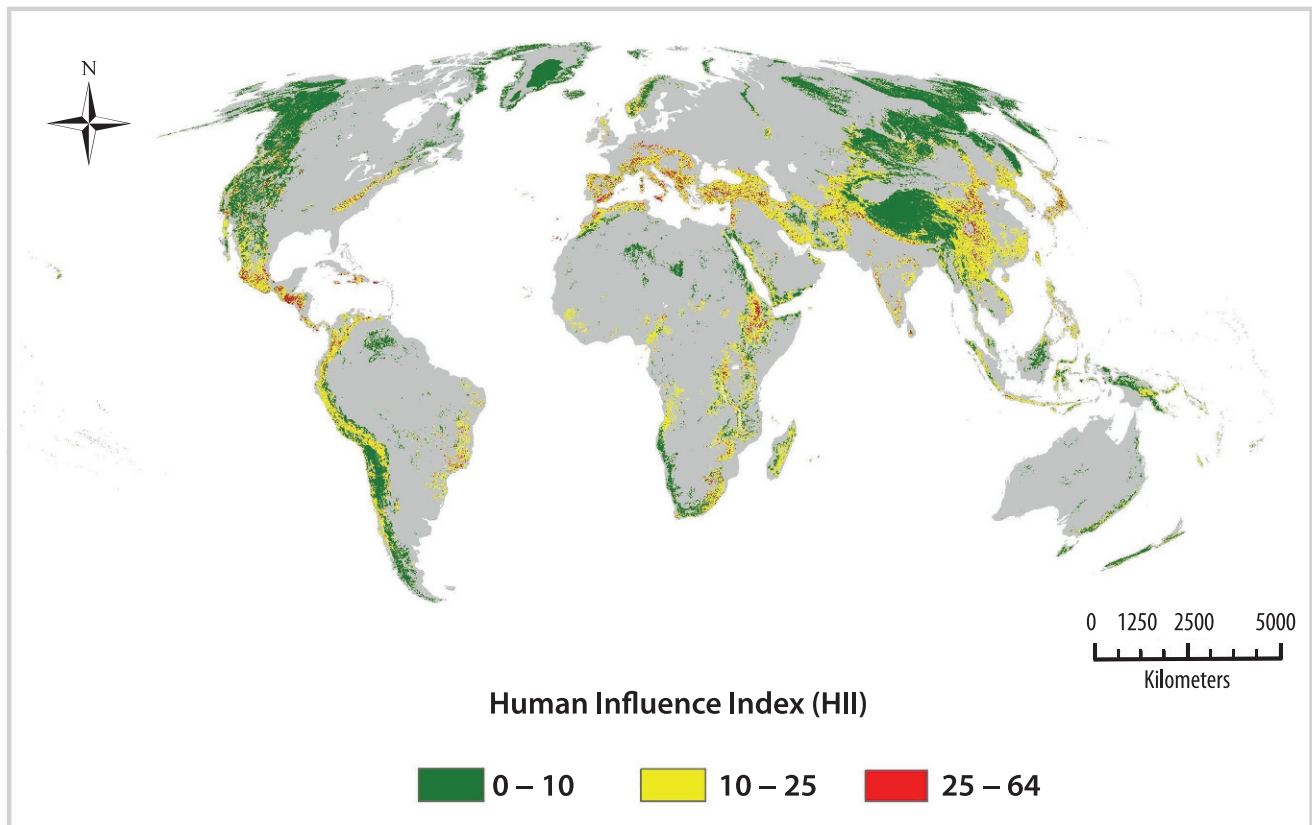
The degree of human influence on mountains worldwide is moderately low (HII mean = 10.9, SD = 8.5), ranging from a minimum of 0 to a maximum of 64 per pixel. Out of the more than 33.2 million km² of mountain area outside Antarctica, 52.9% are under low human influence ($HII \leq 10$), 40.6% are under moderate human influence ($10 < HII < 25$), and 6.5% are under high human influence ($HII \geq 25$). More than 4.7 million km², or 14.3% of all mountain areas outside Antarctica, are under no direct human influence ($HII = 0$).

Most of the largest “wildest” mountain areas ($HII \leq 10$) lie at high northern latitudes, for example, in Alaska, Canada, Greenland, the Scandinavian Peninsula, and the Russian Federation (Figure 1). At medium or low latitudes, other large relatively undisturbed mountain areas are in the United States, the Andes and Venezuelan-Guiana Highlands in South America, northern and southern Africa, the Himalayas and the Tibetan Plateau in Asia, and most mountain areas in Oceania: Borneo, Papua New Guinea, Australia, and New Zealand.

The most influenced mountain areas spread along Central America, northwestern South America, southern central Europe and the Mediterranean, northern and eastern Africa, the Middle East, and far eastern continental Asia and Japan.

Out of the approximately 17.6 million km² of mountain area under low human influence ($HII \leq 10$), some 6.1 million km² (34.7%) are currently covered by nationally designated protected areas. (Figure 2). Protected areas cover large relatively undisturbed mountain areas in western North America, South America, Greenland, the Scandinavian Peninsula, continental Asia, Australia, and New Zealand. However, mountain areas under low human influence in other parts of the world are not yet protected, for example, in continental Asia, the Arabian Peninsula, and parts of Africa.

FIGURE 1 Human influence on the world's mountain areas as measured by the Human Influence Index (HII). (Map by authors)



Discussion

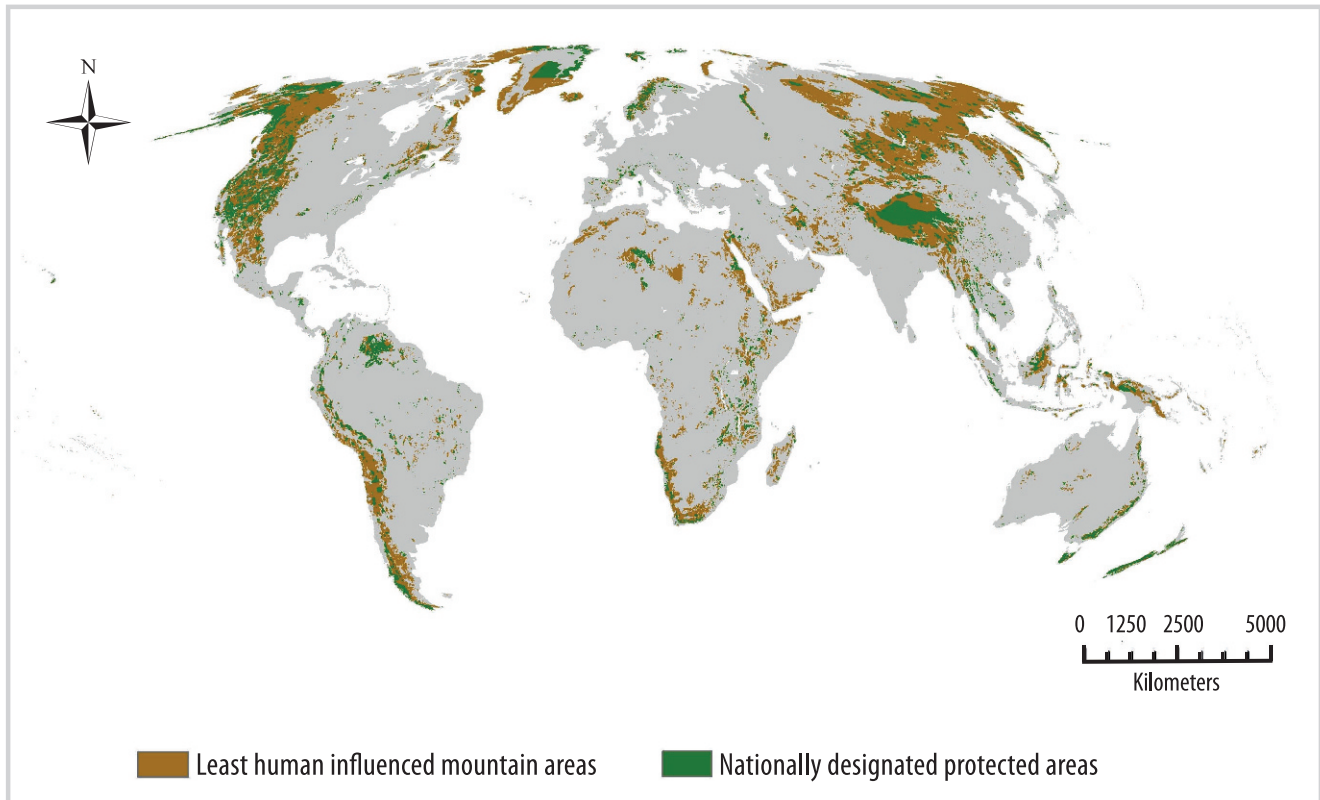
The degree of human influence on the world's mountains, as measured by the HII, is low overall. More than half of all mountain areas are under low direct human influence, and only 6.5% of the world's mountain areas are under high direct human influence, though these figures vary notably among regions and mountain ranges (Burgess et al 2007; EEA 2010b). Unsurprisingly, the most heavily influenced mountain areas corresponded largely to the most densely populated regions in the world (Sanderson et al 2002). The relative remoteness and harsh living conditions of most mountains determine generally low values for two of the variables forming the HII: population density and accessibility. These considerations also influence moderate values for the other two variables: electric power infrastructure and land transformation. In fact, this last variable has evolved in an overall positive way in some regions of the world, such as Europe, in recent years as a result of marginal land abandonment, reforestation and better management of resources (EEA 2010b).

Interestingly, areas under no direct human influence (HII = 0) contribute less to the world's mountain areas (14.3%) than to the global terrestrial surface (17%,

according to Sanderson et al 2002). This is a result of the vast extent of remote and unpopulated areas outside the world's mountain areas, such as the boreal forests and Arctic tundra of Canada and Russia; the largest world's deserts in Northern Africa, Australia, the Arabian Peninsula and Asia; and the Amazon basin (Sanderson et al 2002). On the other hand, our analysis shows that a number of high-biodiversity mountain areas around the world, for example, in the Mediterranean, Mesoamerica, and Africa, are under relatively high direct human influence. For sub-Saharan Africa, Burgess et al (2007) showed that high-biodiversity mountain areas have higher levels of human influence than the mean across the whole region. At the global level, our overall value of human influence on mountains (HII = 10.9) is slightly higher than the value reported by Kier et al (2009) for the world's mainlands (HII = 9.8) but considerably lower than their value for the world's islands (HII = 15.7).

By the end of 2009, 16.9% of the world's mountain areas outside Antarctica were protected, compared to 12.9% of the total land area outside Antarctica (Rodríguez-Rodríguez et al 2011). Considering only the least influenced mountain areas, the proportion protected increases to more than a third (34.7%), a value that by far exceeds current protection levels in any major

FIGURE 2 Protected area coverage of the least influenced mountain areas ($HII \leq 10$). (Map by authors)



region or biome (Jenkins and Joppa 2009; UN 2011). The world's protected areas are clearly biased toward mountain areas, especially those under the least human influence (Joppa and Pfaff 2009, 2011). However, protected area coverage is highly uneven across the world's mountains and inadequate at a range of scales, including areas of particular importance for biodiversity (Rodríguez-Rodríguez et al 2011).

Although we used the best available global data, our analysis likely somewhat underestimates the true extent of human influence and protected areas in mountains. Updating global databases regularly is challenging, expensive, and often inaccurate (Sanderson et al 2002), because data are often collected by different sources using different methods on a sporadic or even on a one-off basis. The databases used to build the HII (SEDAC 2005b) were the most complete and accurate data sources at the time. However, changes in population density, land transformation, accessibility, or electrical power infrastructure in some mountain areas of the world have occurred since HII construction and are not reflected in the current analysis. Similarly, our results may have been affected by gaps in the protected areas data, for example, concerning recently established protected areas that have not yet been reported to the WDPA. In addition, the current analysis excluded a few dozen protected areas whose area is unknown, as well as all internationally designated protected

areas, which is common practice at present (Jenkins and Joppa 2009, 2010; Rodríguez-Rodríguez et al 2011). Finally, it is important to stress that the HII and our analysis consider only direct human impact on mountains, not major indirect human impacts especially relevant to mountain areas, such as climate change or airborne pollution (UNEP-WCMC 2002; Kohler and Maselli 2009; Macchi 2010).

Further research on the topic of direct human influence on mountain areas should take into account other important variables to provide more meaningful results for the conservation and sustainable development of mountain areas. Additional analyses should look at the variation of the HII across different mountain classes (UNEP-WCMC 2002), protected area management categories (Dudley 2008; Jenkins and Joppa 2010), and biogeographical units (eg Olson et al 2001). Mountain ecosystems and livelihoods are among the most vulnerable to global change (Price and Butt 2000; Kohler and Maselli 2009; Macchi 2010), which threatens sustainable development in mountains (Macchi 2010). Factors complementary to the 4 variables making up the HII, such as climate change, are leading to ecological and socioeconomic degradation, causing higher extinction rates and increased exposition to extreme events and natural hazards, exacerbating poverty, and jeopardizing food security, especially in rural communities of developing countries (Macchi 2010). Thus, other forms of human influence on the drivers and consequences of global change

should be studied and addressed through adaptation and mitigation measures, such as the targeted expansion of the protected area system aimed at the conservation of the range of ecosystem goods and services provided by mountain areas (Dudley et al 2010; Rodríguez-Rodríguez et al 2011).

Conclusions

Many mountain areas around the world continue to support “wild” nature. By the early 2000s, direct human influence on the world’s mountain areas was still low overall, except in the most densely populated regions. As a result, most mountain areas could still be deemed relatively “wild,” a characteristic mountains share with few of the world’s ecosystems (Sanderson et al 2002; Hoekstra et al 2005; Ellis and Ramankutty 2008). However, mountain ecosystems are changing rapidly, and these changes are likely to have profound effects on the critical ecosystem goods and services provided by mountains (Kohler and Maselli 2009; EEA 2010b; Macchi 2010). New monitoring programs, including improved and updated global datasets on both direct and indirect human impacts on mountain ecosystems, are therefore needed to regularly assess the state of the world’s mountains beyond the snapshot analysis provided here.

Overall, mountain areas are comparably well covered by protected areas (Kollmair et al 2005; Rodríguez-Rodríguez et al 2011), and this is especially true for the least influenced mountain areas, as we have shown here. However, mountain protection is highly uneven across different scales, and at present, it falls short of internationally agreed-upon targets in many mountain areas (Rodríguez-Rodríguez et al 2011). Well-designed, well-located, well-managed, and well-connected protected

areas are still considered to be among the most effective instruments to conserve important biodiversity and ecosystem services (CBD 2010). Hence, it is critical to fill existing gaps in the protection of important mountain areas (Rodríguez-Rodríguez et al 2011). Such gaps include a number of Alliance for Zero Extinction sites in mountain areas, where highly threatened species are confined to single sites (Ricketts et al 2005; Butchart et al 2010).

Additional protected areas should target primarily areas where they are expected to have the greatest potential impact on the conservation of biodiversity and complementary ecosystem services (Joppa and Pfaff 2009, 2011). While remote mountain areas under no or little direct human influence represent low-hanging fruit for the expansion of protected area systems, they are unlikely to contribute as much to the ongoing efforts to halt the loss of biodiversity and other ecosystem services as protected areas in regions under high human influence (Myers et al 2000; Hoekstra et al 2005; Ricketts et al 2005; Joppa and Pfaff 2009, 2011), which are more at risk and for which sustainable development policies and practices are specially needed. We hope that our preliminary map of direct human impact on the world’s mountain areas will contribute to the ongoing identification of future conservation priorities in mountain ecosystems. Even though a targeted expansion of the protected area in mountains remains a priority (Rodríguez-Rodríguez et al 2011), an integral approach to the conservation of the goods and services provided by mountain regions must also address global indirect human impacts through international studies, agreements, and regulations. Without both complementary approaches, the world’s mountain goods and services will continue to be degraded or lost.

ACKNOWLEDGMENTS

We acknowledge all the people who contributed to the WDPA, to the global datasets used to compile the HII, and to the organizations managing them. We also thank the anonymous reviewers, whose views helped improve the quality of this work.

REFERENCES

- Burgess ND, Balmford A, Cordeiro NJ, Fjeldsà J, Küper W, Rahbek C, Sanderson EW, Scharlemann JPW, Sommer JH, Williams PH.** 2007. Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biological Conservation* 134:164–177.
- Butchart S, Walpole M, Collen B, Van Strien A, Scharlemann J, Almond R, Baillie J, Bomhard B, Brown C, Bruno, J, Carpenter K, Carr G, Chanson J, Chenery A, Csirke J, et al.** 2010. Global biodiversity: Indicators of recent declines. *Science* 238:1164–1168.
- CBD [Convention on Biological Diversity].** 2004. *COP 7 Decision VII/27: Mountain Biological Diversity*. Montreal, Canada: CBD. www.cbd.int/decision/cop/?id=7764; accessed on 1 April 2012.
- CBD [Convention on Biological Diversity].** 2010. *COP 10 Decision X/2: Strategic Plan for Biodiversity 2011–2020*. Montreal, Canada: CBD. www.cbd.int/decision/cop/?id=12268; accessed on 1 April 2012.
- Dudley N, editor.** 2008. *Guidelines for Applying Protected Area Management Categories*. Gland, Switzerland: IUCN [International Union for Conservation of Nature].
- Dudley N, Stolton S, Belokurov A, Krueger L, Lopoukhine N, MacKinnon K, Sandwith T, Sekhran N, editors.** 2010. *Natural Solutions: Protected Areas Helping People Cope with Climate Change*. Gland, Switzerland: IUCN-WCPA [International Union for Conservation of Nature—World Commission on Protected Areas], TNC [The Nature Conservancy], UNDP [United Nations Development Programme], WCS [Wildlife Conservation Society], World Bank, and WWF [World Wildlife Fund].
- EEA [European Environment Agency].** 2010a. *EEA Report No. 5/2010. Assessing Biodiversity in Europe: The 2010 Report*. Luxembourg: Office for Official Publications of the European Union.
- EEA [European Environment Agency].** 2010b. *EEA Report No. 6/2010. Europe’s Ecological Backbone: Recognising the True Value of our Mountains*. Luxembourg: Office for Official Publications of the European Union.
- Ellis EC, Ramankutty N.** 2008. Putting people in the map: Anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* 6(8):439–447.
- Hoekstra JM, Boucher TM, Ricketts TH, Roberts C.** 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters* 8:23–29.
- IUCN and UNEP-WCMC [International Union for Conservation of Nature and United Nations Environment Programme—World Conservation Monitoring**

- System].** 2010. *The World Database on Protected Areas (WDPA): January 2010*. Cambridge, United Kingdom: UNEP-WCMC.
- Jenkins CN, Joppa L.** 2009. Expansion of the global terrestrial protected area system. *Biological Conservation* 142:2166–2174.
- Jenkins CN, Joppa L.** 2010. Considering protected area category in conservation analyses. *Biological Conservation* 143:7–8.
- Joppa LN, Pfaff, A.** 2009. High and far: Biases in the location of protected areas. *PLoS ONE* 4(12): e8273. <http://dx.doi.org/10.1371/journal.pone.0008273>.
- Joppa LN, Pfaff, A.** 2011. Global protected area impacts. *Proceedings of the Royal Society B* 278:1633–1638.
- Kier G, Kreft H, Lee TM, Jetz W, Ibsch PL, Nowicki C, Mutke J, Barthlott W.** 2009. A global assessment of endemism and species richness across island and mainland regions. *PNAS* 106(23):9322–9327.
- Kohler T, Maselli D, editors.** 2009. *Mountains and Climate Change: From Understanding to Action*. Bern, Switzerland: Geographica Bernensia.
- Kollmair M, Gurung G, Humi K, Maselli D.** 2005. Mountains: Special places to be protected? An analysis of worldwide nature conservation in mountains. *International Journal of Biodiversity Science and Management* 1:181–189.
- Macchi M.** 2010. *Mountains of the World: Ecosystem Services in a Time of Global and Climate Change*. Kathmandu, Nepal: ICIMOD [International Centre for Integrated Mountain Development].
- McNeill JR.** 2000. *Something New Under the Sun: An Environmental History of the Twentieth-Century World*. New York, NY: Norton.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J.** 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- Olson DM, Dinerstein E, Wikramanake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR.** 2001. Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51:933–938.
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM.** 1995. The future of biodiversity. *Science* 269:347–350.
- Price MF, Butt N, editors.** 2000. *Forest in Sustainable Mountain Development: A State-of-Knowledge Report for 2000*. Wallingford, United Kingdom: CABI Publishing.
- Ricketts TH, Dinerstein E, Boucher T, Brooks TM, Butchard SHM, Hoffmann M, Lamoreux J F, Morrison J, Parr M, Pilgrim JD, Rodrigues ASL, Sechrest W, Wallace GE, Berlin K, Bielby J, et al.** 2005. Pinpointing and preventing imminent extinctions. *PNAS* 102:18497–18501.
- Rodríguez-Rodríguez D, Bomhard B, Butchart SHM, Foster MN.** 2011. Progress towards international targets for protected area coverage in mountains: A multi-scale assessment. *Biological Conservation* 144(12):2978–2983.
- Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, et al.** 2000. Global biodiversity scenarios for the year 2010. *Science* 287:1770–1774.
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G.** 2002. The human footprint and the last of the wild. *BioScience* 52(10):891–904.
- SEDAC [Socioeconomic Data and Applications Center].** 2005a. *Last of the Wild Data Version 2 (LWP-2): Global Human Footprint Data Set (HF)*. New York, NY: WCS [Wildlife Conservation Society] and CIESIN [Center for International Earth Science Information Network]. <http://sedac.ciesin.columbia.edu/wildareas/downloads.jsp#Humfoot>; accessed on 30 March 2012.
- SEDAC [Socioeconomic Data and Applications Center].** 2005b. *Last of the Wild Data Version 2 (LWP-2): Global Human Influence Index (HII)*. New York, NY: WCS [Wildlife Conservation Society] and CIESIN [Center for International Earth Science Information Network]. <http://sedac.ciesin.columbia.edu/wildareas/downloads.jsp#infl>; accessed on 30 March 2012.
- UN [United Nations].** 1992. *Agenda 21. The United Nations Programme of Action from Rio*. New York, NY: UN. www.un.org/esa/dsd/agenda21/; accessed on 11 May 2010.
- UN [United Nations].** 2011. *The Millennium Development Goals Report 2011: Statistical Annex*. New York, NY: UN.
- UNEP-WCMC [United Nations Environment Programme—World Conservation Monitoring System].** 2002. *Mountain Watch: Environmental Change and Sustainable Development in Mountains*. Cambridge, United Kingdom: UNEP-WCMC.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM.** (1997). Human domination of Earth's ecosystems. *Science* 277:494–499.