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Mountain gloom and mountain glory revisited: A survey of conservation, connectivity, and climate change in mountain regions

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ABSTRACT

Mountain regions have played a significant role in the history of biodiversity conservation, and promise to play an even larger part in future efforts to respond to climate change. After an historical overview of scientific research into mountain ecosystems, biodiversity conservation in mountain regions is examined in light of the ever-expanding research agenda on *landscape connectivity* and *corridor ecology*. An array of potential beneficial and deleterious effects of 'wildlife corridors' is then discussed, along with a description of the conceptual scientific underpinnings of wildlife corridors in the field of island biogeography, metapopulation dynamics, and landscape ecology. The effects of climate change on mountain ecosystems are then reviewed, focusing on the premise that the protection and restoration of corridors constitute the most comparatively effective prospect for protecting mountain biodiversity in the long term. We conclude that three distinct research communities—the mountain research community, the corridor ecology community, and the climate change community—will have to provide mutual support in answering four critical questions: (1) What do we need to know about mountain biodiversity and how it interacts with human communities in the mountains? (2) In what ways can the establishment of 'on-the-ground' corridors provide sufficient connectivity between 'natural' communities, species, and populations in mountain regions? (3) To what degree will anthropogenic climate change require us to modify our response to the first two questions? (4) How can we best build resilience into mountain ecosystems?

Keywords: anthropogenic climate change, core areas, corridor ecology, corridor effectiveness, island biogeography, landcape connectivity, landscape ecology, metapopulation dynamics, mountain ecosystems, resilience

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MOUNTAIN CORRIDORS IN CONTEXT: A HIGH-ALTITUDE CONVERGENCE OF SCIENTIFIC ENDEAVORS

From space, a view of Earth reveals scores of mountain ranges criss-crossing the continents. From low ground, mountains dominate the landscape wherever they are found—indeed, one definition of mountains relies on the word 'conspicuous.' From either perspective, the human eye cannot help but be drawn to the high mountain terrain that covers approximately 27% of the Earth's surface (Rodńguez-Rodńguez *et al.* 2011; see also Chape *et al.* 2008; Diaz *et al.* 2003; Kapos *et al.* 2000; La Sorte and Jetz 2010). Whether this high terrain induces dread or aspiration—mountain gloom or mountain glory, to paraphrase the title of Nicolson's (1959) classic text—it is not surprising that mountain views have inspired myriad forms of cultural lore and traditions, revealing a widely shared awe for the high country through the assignation of revered, feared, sacred, and protected status for mountains worldwide (Bernbaum 1997, 1998).

Mountain ranges have also directly influenced the patterns of settlement and movement by both humans and wildlife. They act variously as barriers to movement, as sources of seasonal resources at different elevations, and as navigational reference points. In the first case, mountain chains serve to limit the range of particular species and populations—limits that are often described as international borders (or 'geopolitical boundaries') in the case of *Homo sapiens*. In terms of food resources, mountains allow for altitudinal seasonal migration that enables the sustenance of larger populations (be they of the domestic cow or the wild grizzly bear) than could otherwise exist. Thirdly, mountain terrain not only provides navigational assistance, but directly influences travel routes. Two very different examples are many migratory birds, which rely on mountain updrafts for their long seasonal migrations, and humans, whose transportation infrastructure is highly influenced by mountains (from the ancient Silk Road to the U.S. interstate highway system).

Although somewhat protected by their inaccessibility, mountain regions today increasingly face the same litany of threats that have extended the human footprint over more than 80 percent of the world's land area (excluding Antarctica; see Sanderson *et al.* 2002). Moreover, even for those areas that have received some type of protected status, an oft-heard desultory refrain in the conservation community holds that governments have done an above-average job of protecting the 'rock and ice' of the world's mountains. Implicit in such an acerbic compliment is the notion that we have protected the land least susceptible to development pressure—the lands nobody wanted all that much. Such an uninformed critique underestimates the significance and extent of the human cultures and the genetic, species, and ecosystem diversity in alpine and highland regions—as well as their function as the important headwater resources for most of the rivers of the world. However, the critique is on target at least to the degree that there remains insufficient protection for the full range of important low-to-high elevation habitats worldwide. There are at least 21,400 protected areas in mountains (as defined by Kapos *et al.* 2000), constituting roughly 32 percent of the global protected areas estate and covering 17 percent of the total mountain area outside of Antartica (Rodŕıguez-Rodŕıguez *et al.* 2011; see also Hamilton 2006).

The formal establishment of protected areas in mountain regions is tightly interwoven into the complex tapestry of conservation history. Notably, many of the world's earliest protected areas were established in mountain environments. Why mountains received such attention is a matter of long-standing consideration and debate, with proposed causal chains involving a number of topographical and anthropological factors. Some argue that these early protection efforts reflected romantic sensibilities over the sublimity of nature as manifested in lofty peaks; others that such inaccessible 'waste lands' were hardly useful for any practical purpose beyond scenery, recreation, or tourism. Some found that business interests were critical in tying together romantic ideals with tourism dollars; still others rejoined that at least some of the practical benefits of mountain conservation were well understood early on (see Lowenthal 2000; Marsh 1864 [1965]; Nicolson 1959; Purchase 1999; Runte 1987). For instance, as early as 1892 the state of New York established an Adirondack Park (over 2.8 million acres of largely mountainous public and private lands) in order to safeguard headwaters of many of the state's rivers and canals (Hamilton *et al.* 1982; Schneider 1997, 224–225). An even earlier example comes from China; one of the authors has a print of a painting showing reforestation of mountains in China in the 16th century for 'river conservancy.'

From a broad historical perspective, these particular positions over causation would become enmeshed (one might say entrenched) in the simplistic ideological dichotomy between 'preservation' and 'conservation'—the former referring to placing nature off-limits to human interference, the latter to protecting natural resources for people through wise management. Although these 'sides' are historically portrayed as having been in conflict, they have arguably often played mutually supportive roles in political and policy debates over 'nature protection.' Whatever the case, whether it be under the rubric of 'mountain biodiversity protection' on the one hand or 'sustainable mountain development' on the other, mountain regions have been central in broader debates over the accurate characterization of global conservation efforts.

In general, it is probably fair to say that most conservation practitioners view the dichotomy between 'preservation' and 'conservation' as false (hundreds of publications have examined this topic; for a relatively concise examination, see Manuel-Navarrete *et al.* 2006; for an extended treatment, see Wellock 2007). Yet as can be detected in a review of the handful of extant globally-focused mountain conservation initiatives (see Box 1), the distinction remains relatively discernable. On the one hand, a number of these initiatives focus directly on the preservation of mountain landscapes and biodiversity; on the other, a number of initiatives focus on sustaining the human environment in the mountains, holding biodiversity protection as but one of numerous components within a broader development mission. So even as these two worlds overlap significantly in terms of content and context, a certain level of tension remains over where and when humans should and should not be part of the conservation equation (e.g., Chapin 2004; Hamilton 1996).

Over the course of the coming decade, the dichotomy is likely to further dissipate due to increasing insights emanating from the two scientific arenas of *climate change* and *corridor ecology*. Although occurring at very different scales, the growth of investigations within these two fields has been dramatic over the past decade. First, the growing body of research on the effects of climate change on biodiversity has entailed a strong focus on the dramatic vegetation and habitat changes that could occur within mountain environments. As but two policy-significant examples, a great deal of attention has been given to the fate of (1) the high-elevation, temperature-sensitive American pika (*Ochotona princeps*) and (2) the snow-pack dependent wolverine (*Gulo gulo*). Although pika populations have been found to be more resilient in responding to climate variability than previously believed (Millar and Westfall 2010), researchers nonetheless remain concerned about the fate of individual pika populations and their ability to connect to suitable habitats (Beever *et al.* 2010; for an overview of the effects of climate change on the pika, see Ray *et al.* 2012). In the case of the wolverine, which typically depends on cool places both to cache their food where it will not rot and to den in areas where deep snow provides insulation, the loss of permanent snow could be highly problematic. In an extensive and intensive examination of North American wolverines in mountainous regions, McKelvey *et al.* (2011) caution that continuing 'warming trends may create many small and isolated populations that would be subject to high levels of demographic and genetic stochasticity.'

Second, the fields of conservation biology and landscape ecology have seen the recent coalescing of shared sub-disciplines into the emerging practice of *corridor ecology* (also referred to as *connectivity conservation*), within which mountain regions have received significant attention. Mountain ranges, both north–south (the Andes) and east–west (the Himalayas) offer conceptually straightforward natural corridors, usually consisting of relatively less human-modified large landscapes. Each of these scientific disciplines has raised the prospect of rapid and impending changes—changes that threaten to overshadow any single-minded focus on either 'mountain biodiversity protection' or 'sustainable mountain environments.'

In light of these scientific developments, we review the central propositions of the sciences of corridor ecology and climate change as they relate to mountain environments. But before turning to examine them, it would be remiss to overlook the historical development of a third scientific endeavor that largely predates the other two—one that has been generically labeled 'mountain research,' but might be more descriptively denoted as 'the science of mountain environments.' Although our review can only provide a mere keyhole view onto this extensive field of study, understanding the basic historical backdrop of this foundational scientific endeavor constitutes a key initial step in assessing future prospects for mountain regions.

AN ABBREVIATED HISTORY OF SCIENTIFIC RESEARCH ON MOUNTAIN ENVIRONMENTS

Scientific research on mountains has a long and rich history, but just how long and rich depends on what constitutes science. One might go as far back as Aristotle, who in the fourth century BCC considered the role of mountains in stream formation (Nicolson 1959, 164–165). Two millennia later, one of the 'most violent' scientific controversies of the Enlightenment concerned the origins of glaciers, the evidence for which was largely encountered in mountain environments (Imbrie and Imbrie 1979). While the formal study of the relationship between humans and mountain environments is typically dated to the end of the 19th century, some observers trace the science of mountains 'in the "Western context"' to Alexander von Humboldt's travels in the Andes during the dawning years of the 19th century, when he recognized the relationship between latitude, elevation, and 'distinctive altitudinal belts' (Ives *et al.* 1997, 4).

Over the 20th century, one of the more prominent figures in mountain research was the German biogeographer Carl Troll, whose work led him to coin the terms 'landscape ecology' and 'geoecology' (the latter term being Troll's replacement for the former, but which came to take on a number of varied meanings at least partly in regard to 'the consideration of changes in the Earth's geospheres caused by human activity'; Trofimov 2008, 65). Troll was instrumental in the establishment of a number of mountain research initiatives, one of the most significant of which was a 1966 symposium on the tropical mountains of the Americas. This event in turn led to the 1968 establishment of the Commission on High Altitude Geoecology of the International Geographical Union, which had the 'objective of extending the work on the tropical Americas to embrace all the high mountain systems of the world' (Ives 1973, A1). As noted in Box 1, which presents a chronological listing of some of significant events in mountain research since the late 1960s, these two initiatives were the forerunners of an extensive number of mountain research initiatives over the ensuing decades. Box 1 is hardly a complete listing; the point is that there is a diverse community of researchers working under the aegis of a discernable scientific discipline focused on mountain environments.

Until the 1980s, most natural and social scientists working in mountains were focused solely on their own discipline, quite often 'loners' in their particularized pursuits. The initiation of the International Mountain Society (IMS) by Dr. Jack Ives in 1980 began a process of both knitting together mountain scholars into a community and promoting multi-disciplinary research on common problems—objectives very similar to those that had already been envisioned in the Man and the Biosphere Program's Mountain Project of 1973 (see Ives and Messerli 1990). In 1981, IMS established the journal *Mountain Research and Development*, which to the present day has provided an arena for a wide array of mountain studies.

Following a milestone mountains meeting at Mohonk Mountain House (New York) in 1986 (see Box 1), five of these IMS scholars determined to attempt the task of placing mountains as a major earth feature and significant biome on the world's political agenda. Specifically, Drs. Yuri Badenkov, Jayanta Bandhopadhyay, Lawrence Hamilton, Jack Ives and Bruno Messerli formed a group called 'Mountain Agenda', which would be augmented by Rudy Hoegger of the Swiss Development Agency supported by Dr. Maurice Strong, the first Executive Director

Box 1 A chronological listing of some of the major mountain research developments since the late 1960s, particularly in reference to corridors and climate change

1966: First symposium on the geoecology of mountainous regions held in Mexico under the sponsorship of UNESCO

1968: International Geographical Union (IGU) establishes 'Mountain Commission' (formally, the Commission on High Altitude Geoecology, subsequently renamed (1) Mountain Geoecology and Resource Management, (2) Mountain Geoecology and Sustainable Development, and (3) Diversity in Mountain Systems)

1973: Establishment of Project 6 of UNESCO's Man and the Biosphere Program: Study of the Impact of Human Activities on Mountain (and Tundra) Ecosystems

1974:
- Alpine Areas Workshop sponsored by the International Institute for Applied Systems Analysis, representing collaboration between the IGU Mountain Commission (see 1968) and UNESCO MAB 6 (see 1973), leading to the UN University mountain project (see 1977) and the establishment of the International Mountain Society (see 1980)
- Publication of *Geoecological Relations between the Southern Temperate Zone and Tropical Mountains* (Troll and Laver 1978) under the IGU Mountain Commission

1975: International Workshop on the Development of Mountain Environments

1977: Establishment of the United Nations University (UNU) project on Highland–Lowland Interactive Systems (now Mountain Ecology and Sustainable Development)

1980: Establishment of the International Mountain Society (IMS) leading to establishment of the catalytic journal *Mountain Research and Development* (1981–present)

1983: Establishment of the International Centre for Integrated Mountain Development (ICIMOD) in Kathmandu, Nepal

1984: Mountain Commission publishes *Natural Environment and Man in Tropical Mountain Ecosystems* (Lauer 1984)

1986: Mohonk Mountain Conference on *Himalaya-Ganges Problem* leading to formation of a group called 'Mountain Agenda' dedicated to putting mountains on the global agenda

1988: Feasibility study at the East-West Center (Hawaii) for an International Mountain Research and Training Structure

1989: *The Himalayan Dilemma: Reconciling Development and Conservation* published, bringing science to bear on misinformation about mountain uses and development (Ives and Messerli 1989)

1990:
- Publication of *Sacred Mountains of the World* (Bernbaum 1990)
- Initiation of 'Paseo Pantera' (in Central America, first large bioregional mountain conservation corridor initiative, later re-envisioned as the Mesoamerican Biological Corridor)

1991: Seven European countries and the EEC sign the Alpine Convention, putting in place policies on protection of the European Alps

1992:
- Publication of two documents by 'Mountain Agenda' aimed at the UN Conference on Environment and Development's Agenda 21: *An Appeal for the Mountains* (Mountain Agenda 1992) and *The State of he World's Mountains* (Stone 1992)
- Mountain Biome Theme established under IUCN's World Commission on Protected Areas
- Chapter 13 of Agenda 21 is approved, entitled: *Managing Fragile Ecosystems: Sustainable Mountain Development*
- European Habitat Directive issued by the European Communities, with signficiant implications for conservation of European alpine habitat

1993: 'Yellowstone to Yukon' first conceived as a global model for mountain conservation

1994: Mountain Institute sponsors NGO workshop on Mountain Agenda at Spruce Knob, West Virginia

1995:
- Formation of the Mountain Forum global network in Lima, Peru
- Publication of *Tropical Montane Cloud Forests* (Hamilton *et al.* 1995), the first global assessment of this ecosystem

1997: Publication of *Mountains of the World: A Global Priority* (Messerli and Ives 1997)

1999: Global Observation Research Initiative in Alpine Environments (GLORIA) established in Europe; since expanded to a global network of projects

2000:
- International Geographic Union establishes a Commission on Diversity in Mountain Systems
- Global Mountain Biodiversity Assessment established under DIVERSITAS

2001: Establishment of the Mountain Research Initiative (the origins of which can be dated to a 1996 conference and earlier work), with major research component on global change and climate change

2002:
- UN declared International Year of Mountains (IYM) with scores of national events held by most countries with mountains
- Publication of *Mountain Biodiversity: A Global Assessment* (Körner and Spehn 2002), with an extensive section on climate change
- Establishment of the International Partnership for Sustainable Development in Mountain Regions ['Mountain Partnership'] serviced by the UN Food and Agriculture Organization (FAO)

2003: Global Change in Mountain Regions (GLOCHAMORE) initiated

2005: Chapter on 'Mountain Systems' in Millennium Ecosystem Assessment: Conditions and Trends Working Group Report (Hassan *et al.* 2005, Chapter 24)

2006: Papallacta Declaration on Mountain Connectivity Conservation

2008: IGU establishes Commission on Mountain Response to Climate Change

2010: Publication of *Connectivity Conservation Management: A Global Guide* (Worboys *et al.* 2010), containing a strong focus on mountain ecosystems of the UN Environment Programme and who would become the Secretary General of the 1992 UN Conference on Environment and Development (the 'Earth Summit'). By 1992 they had produced two key documents that were placed in front of all delegates to the Earth Summit: a colorful booklet *An Appeal for the Mountains* (Mountain Agenda 1992) and the book *State of the World's Mountains* (Stone 1992). These efforts led to the inclusion of a chapter on mountains in *Agenda 21*, the Summit's extensive statement on sustainable development (United Nations 1993). Entitled 'Managing Fragile Ecosystems: Sustainable Mountain Development,' Chapter 13 represented the first time that mountains had ever appeared in such a multilateral declaration. Although the proposed funding by governments and donors (US$330 million per year) never materialized, Chapter 13 helped to set in place a mantle of endorsement for a number of significant events and institutions for research in the period 1997–2005, some of which are listed in Box 1.

A growing community of mountain researchers has shown that many of the major challenges of mountain conservation across the globe share some similar characteristics, a proposition that was well illustrated in the milestone publication of *Mountains of the World: A Global Priority* (Messerli and Ives 1997; see also Ariza *et al.* 2013). This book was planned and implemented by the Mountain Agenda group (with the addition of Martin Price, a widely published author on mountain issues; see e.g., Price 1999, 2011 & Price *et al.* 2013). One of these simlarities was the accumulation of a large body of information on mountain ecology, much of which would become highly relevant to the concept of mountain corridors. Significantly, mountains were found to host not only high levels of biological diversity but a high degree of endemism—species found nowhere else on the planet—due to unique geological features, assorted hydrological regimes, natural barriers, differing compass aspects, and varying elevational zones that all contributed to a greater complexity of habitats within a relatively small area. Mountain regions also often act as refugia, retaining species that were once widespread (viz., beyond mountains) but whose habitat in low-lying areas has retreated due to human-induced habitat change or persecution (for a review and discussion of 'microrefugia,' see Dobrowski 2011). Mountains are often the last bastions of wild nature amid a sea of lowland human development.

But even as they act as *de facto* refuges, mountain systems are arguably more fragile than many other ecosystems. Harsher climates at higher elevations mean that primary production is slower, which in turn makes recovery from perturbations a longer process. Steeper slopes mean that both 'natural' processes, such as major storm events and wildfires, as well as anthropogenic processes, such as logging, road-cutting, and other human activities, are likely to cause greater erosion. Natural mass erosion events can be fairly common in these dynamic land features, and earthquakes, volcanic activity, and mountain torrents add to comparative volatility of mountain environments. Further, both because some endemic species have relatively small ranges and because individual mountains or mountain ranges may be isolated, even habitat alteration that is confined to a relatively small area can imperil some populations and species.

Other significant threats to mountain ecosystems include acid deposition and long-distance atmospheric transport of persistent organic pollutants followed by biological magnification. A notable example of the former lies in the Adirondack Mountains, where acid deposition has affected at least 700 lakes and ponds (25 percent of its total) (Adirondack Council 1998; see also Jenkins *et al.* 2007). Resource extraction, storage dams, inappropriate land clearing and agriculture, and overgrazing are some other common threats that plague many mountain ecosystems as well (e.g., Lavergne *et al.* 2005). And as we will describe below in more detail, future efforts to protect mountain ecosystems will require grappling with the complicating challenge of climate change, which is known to have a greater immediate impact at both more northerly latitudes as well as higher elevations.

In surveying this growing understanding of mountain ecosystems, it does not take a great deal of ecological insight to comprehend the importance of connectivity to such ecosystems. Moreover, a critical factor in the maintenance of mountain connectivity is the tendency of humans to settle the most fertile valley bottoms—and this includes mountain valleys. As implied in the above reference to 'rock and ice,' most montane protected areas were created to protect the higher and less fertile elevations (Scott *et al.* 2001). Yet the very productivity that makes valleys so attractive to humans also indicates their importance to other species that rely on those areas as either permanent residents or visitors (particularly in terms of wintering range). Scientists have documented that human occupation has affected biotic composition and survivorship in these montane valleys directly through land-use change (see Hansen *et al.* 2002) and by creating movement barriers for some species (Epps *et al.* 2005). As a result, species movement through and among mountain ranges may be diminished or even lost (Berger 2004).

Despite the mountain research community's long record of investigations, it had paid relatively little attention to the idea of connectivity or maintaining corridors in mountain regions up through to the international declaration of *Agenda 21* in 1992. Fortunately this has since changed with many of the 'old guard' in the mountain science community working to collaborate with a host of younger researchers and conservation practitioners to study and understand the role of mountain corridors (Hamilton and McMillan 2004; Hamilton 1999; Harmon and Worboys 2004; Worboys *et al.* 2010). But to understand why mountain ecology and the attendant threats to mountains have generated so much interest in the role of mountain corridors in large landscapes, it is first necessary to understand the general background of the science of 'corridor ecology.'

CONNECTIVITY, CONSERVATION CORRIDORS, AND CORRIDOR ECOLOGY

The scientific study of connectivity and corridors dates at least to the 1940s, and the use of 'movement corridors as a land management technique dates to the early decades' of the 20th century (Chetkiewicz *et al.* 2006; Harris and Scheck 1991). During the 1990s, a good deal of formative research took place in Europe, particularly in the Netherlands where 'ecological networks' gained much theoretical development and even government support (see for instance Bennett 1994). In this context, physical connectivity generally came in the form of hedgerows or linear greenways such as riparian stream buffers rather than large landscape-scale corridors, but connectivity as a concept was nonetheless becoming widely recognized.

Considerable attention and controversy has attended the benefits and costs of corridors in the subsequent decades (Hilty *et al.* 2006; unless otherwise noted, this section is based on the treatment of corridors in this publication, which contains an extensive literature review). In the vast majority of cases, corridors constitute linkages between two 'core areas' of natural habitat. It is noteworthy that by 1984, Harris had spelled this out explicitly in his extensive treatment of forest fragmentation:

> The choice of ideal old-growth or long-rotation management areas cannot be made without knowledge of the existence of riparian strips or suitable alternative corridors. Similarly, the choice of riparian strips and corridors cannot be made without an approximate location of the old-growth and long-rotation islands. This implies that during the planning stage there should be close interactive review of what pattern is ideal and possible at the regional level, with what is ideal and available at the forest level (Harris 1984, 144).

Yet even as substantial treatments of the issue of corridors were available by the early 1990s (see Hudson 1991; Saunders and Hobbs 1991) and a select number conservation organizations such as the Wildlands Project had become early proponents of large landscape corridors (Noss 1994), the concept was slow in gaining international visibility.

In regard to mountain corridors in particular, one of the authors (Hamilton) expedited a two-day workshop on 'Mountain Corridors' at the 1996 World Conservation Congress (IUCN). This led to a 1996 IUCN Resolution (No. 1.38), which emphasized that 'parts of or entire mountain ranges still offer good opportunities to create wildland bioregional-scale corridors, extending over hundreds or even thousands of kilometers, such as the southeastern Australia Great Dividing Range, the Rocky Mountains from Yellowstone to Yukon, and the Andean Bear corridor from Venezuela to Ecuador' (IUCN 1997). Subsequently, IUCN's Commission on National Parks and Protected Areas began advocating mountain conservation corridors in its publications (see Hamilton 1997, 1999). This effort promoted linking established protected areas linking established protected areas through nature-friendly land use management and buffer zones, thereby allowing species to respond effectively to global change. The specific regionally-targeted conservation initiatives under this effort used mountain ranges on 'sky island archipelagos' as planning units. Two prominent on-the-ground mountain corridors included the Yellowstone to Yukon Conservation Initiative (discussed more extensively below) and the Meso-American Biological Corridor (formerly 'Paseo Pantera'). In an IUCN book by Harmon and Worboys (2004) entitled *Managing Mountain Protected Areas: Challenges and Responses for the 21st Century*, a major section was devoted to 'Corridors of Conservation.' In 2010 under the aegis of IUCN's

World Commission on Protected Areas, Worboys *et al.* (2010) produced *Connectivity Conservation Management: A Global Guide*, containing an extensive set of case studies of "lesson learned" from many mountain corridor initiatives.

Despite this early work, it is probably fair to say that the English scientific literature on corridor ecology has only recently come into its own with the 2006 publication of *four* major treatises synthesizing the role of wildlife connectivity and corridors in biodiversity conservation (Anderson and Jenkins 2006; Bennett and Mulongoy 2006; Crooks and Sanjayan 2006; Hilty *et al.* 2006). Given the dual trends of increasing habitat fragmentation and growing concern over the fate of biodiversity, it may only be a matter of time before 'corridor ecology' becomes as familiar an endeavor as, say, 'forest ecology.'

Corridors have been at the heart of a long-standing and sometimes contentious debate in the science of conservation biology, one that can be summarized in the seemingly straightforward question: Exactly how important are corridors for biodiversity conservation? Researchers working in this arena will quickly retort that the question is hardly straightforward due to the wide variability in how different biologists—not to mention different conservationists, land managers, and the general public—interpret the very word *corridor*. The word carries many different connotations, bringing to mind any number of extremely different entities that range from riverways and large 'landbridges' (such as the isthmus of Panama) to urban greenbelts and even unconnected refuges ('stepping stones') for migratory birds (Dobson *et al.* 1999, 131–132). Rather than starting out by thinking about physical corridors, the argument runs, we should first consider the broader concept of *connectivity*.

Connectivity can be defined as 'the extent to which a species or population can move among landscape elements in a mosaic of habitat types' (Hilty *et al.* 2006, 90). Dobson *et al.* (1999, 137–138) divide connectivity into three geographical scales: (1) connectivity between isolated habitat patches, (2) connectivity at the landscape mosaic scale, and (3) connectivity at the regional scale. They argue that the idea of connectivity both better represents 'the goal of maintaining ecosystem viability' and provides more consistent standards such as the 'surprisingly robust genetic rule of thumb' of 'one migrant per generation' (meaning that for small populations of a species to maintain genetic fitness, a single individual with more diverse genes must immigrate once per average generation) (p.143). But more importantly, the idea of connectivity focuses equal attention on both the connection itself (viz., the corridor) and on *what is being connected*—which will most often consist of 'core areas' of habitat that may or may not have received formal protection.

To sum up this line of thought: corridors constitute important conservation tools, but considering them in isolation makes little sense. So when conservationists, biologists, and land managers are considering how to 'establish' a corridor, they need to focus on what role corridors can play in achieving connectivity. Biologists have a specific term for how they think about all of this: *reserve design*. This term can be summarized as the spatial configuration of core areas and connection between these areas, where both cores and connections may fall within formally protected areas or just de facto natural areas. Notably, biologists, they distinguish reserve design from *reserve selection*, which refers to the selection of 'key sites that should be included in a reserve network as core areas' based on a number of criteria—particularly special elements of high conservation value, representation of habitat type, and focal species (Noss *et al.* 1999). Although reserve selection precedes reserve design in theory, only in the past few decades have the optimistic planning formulae implicit in the terms *reserve selection* and *reserve design* begun to play out in the real world—and here mostly in regard to forward-looking conservation NGOs and land trusts, with government agencies slowly coming to the table. But even as the selection of core reserves and corridors has historically occurred in a haphazard manner, the basic point nonetheless remains: when considering the actual establishment or protection of a specific corridor, consideration of the current and predicted adjacent landscape context is of critical importance.

Too much focus on the semantic distinction between *corridor* and *connectivity* can beg the question of what actually needs to be done on the ground to protect biodiversity (Hilty *et al.* 2006, 90). Yet while conservationists should avoid any terminological fray that threatens actual conservation work, distinguishing between connectivity and corridors can offer conceptual clarity to various forms of conservation work. A helpful analog in this regard can be found in the familiar hierarchial framework of *mission, goals*, and *strategies*. Specifically, if biodiversity conservation constitutes the overarching *mission*, connectivity is the particular *goal* (or objective) that leads to achievement of that mission, and a corridor constitutes the particular *strategy* that accomplishes the goal.

Under this framework, both the mission of biodiversity conservation and the goal of connectivity remain, for the most part, constants across the myriad number of mountain conservation initiatives. In terms of strategy, however, the challenge of establishing, restoring, or retaining particular corridors will vary significantly amongst regions. This will be the case both for initiatives where significant progress has already occurred and where conservation initiatives can best be described as inchoate. Consequently, it is important at this level of analysis to consider carefully the multifarious character of 'corridors' in terms of (1) how the term is currently defined, (2) how the concept was historically intuited, and (3) how that intuition became formalized in the biological sub-disciplines of island biogeography, metapopulation theory, and landscape ecology.

As evident in three extant definitions of *corridor* from volume-length treatments of large landscape conservation processes, the differences are largely a matter of emphasis rather than substantive content:

- '. . . any space, usually linear in shape, that improves the ability of organisms to move among patches of their habitat' (Hilty *et al.* 2006, 50);
- '. . . spaces in which connectivity between species, ecosystems, and ecological processes is maintained or restored at various levels' (Anderson and Jenkins 2006, 4); and
- '. . . large, regional connections that are meant to facilitate animal movements and other essential flows between different sections of the landscape' (Dobson *et al.* 1999, 132).

Along with such generic definitions, scientists have parsed the many particular types of corridors into a number of different categorical schemes, five prominent examples of which are summarized in Box 2. In comparing these categorical frameworks, it is worth emphasizing that they do not necessarily contradict each other, but rather that they collectively provide a tangible demonstration that there are many different ways to think about corridors. In addition to the distinctions listed in Box 2, it is worth noting that *corridor* is a common phrase in various human endeavors such as those laying electric utility corridors or road corridors across the landscape. In this context, Soulé (1991) used the phrase 'conservation corridors' to distinguish the type of corridors that biologists think about from, say, the type of corridor a civil engineer thinks about.

While it is important to make the attempt to define 'corridor' (though not to sanctify any particular definition) it is far more illuminating to look back at its intellectual foundations in the two intertwined realms of 'wildlife conservation' and the 'biological sciences' (an inevitable distinction, albeit one that ignores the innumerable biologists who consider themselves practicing conservationists and the vast majority of conservationists who have a better-than-average understanding of biology). In the case of the former, wildlife conservationists have long recognized that habitat is disappearing, that what remains is becoming more and more fragmented, and that the consequent result would entail widespread extirpations and possible extinctions. The principal conservationist response to this challenge has been the establishment of protected areas, of which there are now well over 170,000 covering some 13 percent of the world's terrestrial surface (La Saout *et al.* 2013). Yet even while protected areas can now be found in most parts of the globe, conservationists are wont to emphasize that even this apparently impressive number of protected areas is dramatically insufficient to protect the Earth's biodiversity (and, moreover, that too many are not effectively managed). To fill the gap, the idea of wildlife corridors between protected areas has, in general, made intuitive sense to the wildlife conservation community writ large.

Such conservationist intuitions regarding corridors have been repeatedly justified by biologists, both through empirical investigation and theoretical analysis. Most notably, in 1967, MacArthur and Wilson synthesized and propounded the theory of *island biogeography*, arguing that the number of species on marine islands was directly related to two primary factors: the size of the island and proximity of the island to the mainland. Over the course of the following decades, many biologists applied the theory to habitat 'islands' in a terrestrial context (e.g., mountain tops, forest fragments, isolated wetlands, etc.). Yet despite progress made in understanding how and why species are distributed, biologists generally came to recognize that the theory of island biogeography was far less applicable in a terrestrial context than in a marine one (for a recent argument that the theory of island biogeography has actually served as an impediment to terrestrial conservation, see Franklin and Lindenmayer 2009).

Turning from direct application of the theory of island biogeography, biologists began to focus on the study of connected and unconnected populations—a single population being loosely defined as a *group* of *individuals* of the *same species*

Box 2 Alternative typological definitions of corridor

Scientists and conservationists have put forth numerous definitions of 'corridor.' While these definitions usually do not directly conflict, they generally reflect different aspects of the same phenomenon. To clarify the situation, several broad attempts have been made to provide a standard definition of the term and/or to catalog the various types of corridors. The following summarizes five such approaches to categorizing the various meanings of 'corridor.' In comparing these five approaches, not only does it become clear that 'corridor' connotes many shades of meaning, but that there are significantly different ways to conceptualize how corridors function.

(1) 'Five broad yet overlapping groups of corridors' (Anderson and Jenkins 2006):

- *Biodiversity corridor*: refers to large-scale landscape linkages covering hundreds to thousands of square kilometers.
- *Biological corridor*: same as 'biodiversity corridor.'
- *Corridor networks*: systems of corridors running in multiple directions.
- *Dispersal corridor*: corridors that promote the movements or migrations of specific species or groups of species.
- *Ecological corridor*: corridors that maintain or restore ecological services on which biodiversity conservation depends; alternatively used as a synonym for 'biodiversity corridor.'
- *Habitat corridor*: a linear strip of native habitat linking two larger blocks of the same habitat.
- *Movement corridor*: same as 'dispersal corridor.'
- *Wildlife corridor*: same as 'dispersal corridor.'

(2) 'An alternative and simpler' distinction between 'two basic types of corridors' (Anderson and Jenkins 2006):

- *Linear corridors*: establish or maintain relatively straight-line connections between larger habitat blocks and extend over distances of up to tens of kilometers.
- *Landscape corridors*: maintain or establish multidirectional connections over entire landscapes and can encompass up to thousands of square kilometers.

(3) 'A distinction between different types of habitat corridors based on their origin' (Bennett 2003):

- *Disturbance habitat corridors*: includes roads, railway lines, cleared utility lines, and other linear disturbances.
- *Natural habitat corridors*: includes streams and riparian zones typically following topographic or environmental contours.
- *Planted habitat corridors*: includes farm plantations, windbreaks, and shelterbelts, hedgerows, and urban greenbelts established by humans.
- *Remnant habitat corridors*: includes roadside woodlands ('beauty strips'), linear stretches of unlogged forest within clearcuts, and undisturbed habitats between protected areas.
- *Regenerated habitat corridors*: formerly cleared or disturbed linear strips where vegetation has regrown, such as fencerows and hedges.

(4) 'Three broad kinds of landscape corridor' (Bennett and Mulongoy 2006):

- *Linear corridors*: such as a hedgerow, forest strip or river.
- *Stepping stones*: arrays of small patches of habitat that individuals use during movement for shelter, feeding and resting.
- *Interlinked landscape matrices*: various forms that allow individuals to survive during movement between habitat patches.

(5) 'Types of corridors' (Hilty *et al.* 2006).

- *Unplanned corridors*: landscape elements that enhance connectivity but exist for other reasons.
- *Planned corridors*: established for both biological connectivity and other reasons, planned corridors include:
    - *Greenways*: areas set aside for recreation, culture, and ecosystem services.
    - *Buffering riparian zones*: vegetation growing adjacent to creeks that are sometimes retained in human dominated landscapes.
    - *Corridors for individual species conservation*: often required through mandated management plans for rare and endangered species.
    - *Corridors that enhance community integrity*: promoted to protect biotic community integrity or suites of species moving among parks or protected areas across large regions.

living at the *same* time in the *same area*. A half century of investigations along these lines have been collectively subsumed under the concept of *metapopulations*, defined as 'systems of isolated population units that periodically go extinct ("blink out") and are reestablished ("blink on") by dispersing individuals from other units' (Dobson *et al.* 1999, 151; see also Hanski 1998). Where the theory of island biogeography had focused on the total number of species in a given area, metapopulation theory focused on the fate of a single species. In so narrowing their focus, biologists could use metapopulation theory to think about 'populations of populations'—and that constituted a conceptual breakthrough by treating individual populations, rather than entire species, as generally discrete units. Biologists distinguished between various types of metapopulations and identified various 'metapopulation processes,' with the most important of these being dispersal (to which we will return).

Unlike island biogeography, metapopulation theory explicitly recognized that interactions between habitat patches are highly dynamic—and that the barriers between individual populations may or may not be entirely impermeable. But metapopulation theory has had its own critics. Some pointed out that metapopulation theory had little empirical evidence to show for it (e.g., Anderson and Jenkins 2006) while others argued that it has offered little practical help in terms of identifying on-the-ground conservation priorities (Possingham *et al.* 2001). Dobson *et al.* (1999) summarized one broad critique in noting that 'most species in nature are not as structured as metapopulations in the original sense' and that the original scientific concept of a metapopulation had become so diluted as 'to denote almost any system of populations whether or not they blink out periodically.' In effect, this meant that the concept had little predictive ability and was not likely to be applicable to particular conservation problems (for a recent review of these issues, see Chetkiewicz *et al.* 2006).

Nonetheless, it was this very expansion on the original idea of metapopulations that provided a broad framework for understanding how corridors might function. In order to describe the dynamic processes involved with metapopulations, biologists borrowed three 'especially useful' terms from the field of *landscape ecology*: matrix, patch, and corridor (Forman 1991, 71; 1995). The matrix was originally defined as the dominant landscape type (e.g., forest, city, residential development, etc.) that is determined according to three factors: greatest total area, highest level of connectivity, and strongest 'control over dynamics' (examples of which include seed dispersal, herbivory, keystone predation, and pollutant deposition) (Forman 1995, 277). Patches exist as landscape elements that are both different from and within the matrix. Notably, ecologists today generally take a more nuanced approach to the relationship between these two elements, placing patches within a matrix composed of various types of natural and human-created communities (rather than a single 'dominant landscape type'). Finally, corridors were generically defined as 'a strip of a particular type that differs from the adjacent land on both sides' within the matrix (Forman 1995, 38). As described above, conservation biologists have expanded on that definition, arriving at the broad conclusion that corridors offer a tangible tool for protecting biodiversity in a world where the landscape matrix is increasingly dominated by the loss and fragmentation of habitat due to anthropogenic influences.

With the development of 'corridor ecology' as a discernable scientific endeavor emanating from the three fields of island biogeography, metapopulation theory, and landscape ecology, it is not difficult to understand why so many scientists are conducting research in this area.

The importance of corridors can be also summarized in the single word *movement*—although the phrase *effective movement through the landscape* would be more accurate (a related term, sometimes used in a European context, is 'biopermeability'; see Bona *et al.* 2006; Romano and Zulio 2012). Biologists have long argued that such movement—including daily peregrinations, various types of dispersal, nomadism, and seasonal migrations—is critical to a number of important demographic and genetic processes. Demographic processes include the colonization of new or recovered habitat and the recolonization of habitat where species have been extirpated. Genetic processes include the maintenance of allelic diversity within populations, which can both create greater resilience to changing environmental conditions as well as decrease the risk of inbreeding depression (viz., the 'decreased vigour in terms of growth, survival, or fecundity, that follows one or more generations of inbreeding'; see Rosenberg *et al.* 1997, 679). Effective movement via corridors means that individuals are not deterred or killed by impediments such as roads—a particularly important consideration for species ranging from many amphibians and reptiles to ungulates and large carnivores. Finally, effective movement can also entail the evasion of predation and disease.

Overall, it is the facilitation of movement that constitutes the essential *raison d'être* underpinning corridors. Yet 'effective movement through the landscape' does not cover all of the reasons why corridors are important. Most obvious, although perhaps easiest to overlook, corridors can constitute an increase in or the retention of habitat itself at least for some species (sometimes making it difficult to distinguish between 'core' and 'corridor'; see Dobson *et al.* 1999 and Franklin and Lindenmayer 2009). Related to habitat protection are various ecosystem services such as water filtration and pollution control, and in agricultural regions corridors can provide habitat for important pollinator species, limit pesticide drift, and control populations of pest species. Corridors can also provide recreational opportunities for people and can serve as barriers to the expansion of sprawling urban areas. Finally, and perhaps most significantly, corridors offer potential protection from the effects of climate change (to which we will return after the following section).

EFFECTIVENESS OF CORRIDORS

Do corridors work? Do we know that they will help protect biodiversity if we establish and protect them? By the early 1980s, a number of biologists were answering in the affirmative, basing their arguments in island biogeography. They not only argued that corridors make eminent theoretical sense, but also cited indications—if not empirical evidence—that corridors work, and even noted that corridors represent an 'established wildlife management technique in some regions' (Harris 1984, 141; notably Harris cites a controversial 1977 study that purported to demonstrate the conservation value of a corridor between forest fragments, but 'the study was not a valid test because it lacked replication and did not directly measure the movement of individuals'). Yet in the ensuing decade, the efficacy of corridors for conservation became the subject of considerable contention within the world of conservation biology. Despite the now familiar litany of their potential benefits, multifarious arguments were made *against* corridors—or more specifically, against the idea that corridors only entail positive effects for conservation. A considerable amount of ink would be poured over the issue, and the following review is only a broad overview of the 'corridor controversy' that saw no dearth of vitriolic academic wrangling.

A seminal review by Beier and Noss in 1998 found that a majority of relevant studies published between 1980 and 1997 did not provide conclusive evidence regarding any benefits resulting from corridors. Nonetheless, they did argue that there was sufficient evidence from a select number of well-designed studies that generally supported 'the utility of corridors as a conservation tool' (p. 1249). Furthermore, whatever weaknesses there were in making the case for corridors, Beier and Noss (1998, 1249) also pointed out that: 'No study has yet demonstrated negative impacts from conservation corridors.' A year later, Dobson *et al.* (1999) concluded that with the efficacy of corridors depending on so many factors (including the character of the matrix, the particular species involved, which individuals are moving, the time of year, the degree of movement required to connect populations, and many others), the debate over the efficacy of corridors 'may be sterile because the answers are indubitably yes, no, maybe, or sometimes.'

Since these studies, empirical evidence on corridors has been generally encouraging. In particular, two studies conducted at the Savannah River Site in the United States found strong net benefits to corridors (Damschen *et al.* 2006; Tewksbury *et al.* 2002; the SRS is one of the U.S. Department of Energy's 'National Environmental Research Parks,' see http://nerp.esd.ornl.gov). The more recent study concluded that:

> By providing experimental evidence that corridors increase the number of native plant species in large-scale communities over a wide range of environmental conditions, we show that corridors are not simply an intuitive conservation paradigm; they are a practical tool for preserving biodiversity (Damschen *et al.* 2006, 1286).

Debate over the efficacy of corridors continues (see Hodgson *et al.* 2009 for a critique of connectivity and a rejoinder by Doerr *et al.* 2011), and at times the dialogue moves beyond the biological issues. For instance, Van Der Windt and Swart (2008) illuminate many of the potential political and scientific problems involved in practical applications of the corridor concept. Yet from a biological perspective, the negative effects of most corridors appear to be related to edge effects. Weldon (2006), for example, found that predator activity due to edge effects can reduce the reproductive success of prey populations occupying corridors. Intuitively, this entails lower survivorship of focal species in corridors than core habitats. However, despite lower reproduction or survivorship in marginal corridor habitats, some significant level of connectivity may be achieved—even if to a lesser degree than within a continuous population in core habitat.

In their overview of this debate, Anderson and Jenkins (2006) note that the debate has focused on three primary issues: (1) the scientific evidence for corridor functions, (2) the positive and negative effects of corridors, and (3) the cost-effectiveness of corridors. Hilty *et al.* (2006) delve into more specifics, cataloging thirty 'potential disadvantages of corridors or causes of failure' that have been identified by conservation biologists. Both of these reviews, however, ultimately conclude with what appears to be a general consensus among conservation biologists: viz., that the potential problems of corridors do not negate their benefits. As Hilty *et al.* (pp. 172–173) put it:

> Singly or collectively, these factors can cause corridor projects to fail or be diminished in their effectiveness. Do they add up to a denial of the importance of or efforts to achieve a better-connected world? They do not. While we have attempted to present these possible difficulties as strongly as possible, we believe that in the vast majority of cases the benefits of a corridor will outweigh the negativities.

Given this growing consensus, it would be more efficacious to interpret the potential drawbacks *not* as justification to exclude the protection or establishment of a corridor, but as a standard checklist of issues to take into account when designing and establishing a corridor (Hilty *et al.* 2006, 148). Expressed in this manner, such a checklist would include (but is not limited) to the following criteria:

- The physical structure of corridors should minimize 'edge effects,' such as increased levels of predation and parasitism.
- Corridors should be established to minimize competition with exotic and native invasive species.
- Corridors should not lead to the dilution of locally adapted genes.
- Corridors should not allow local populations to be overwhelmed by immigrants.
- Where populations are small and lack immunity, corridors should not allow for the spread of infectious diseases.
- The opportunity costs associated with establishing and maintaining corridors must be evaluated (e.g., would it be more effective to enlarge core areas?).
- Because corridors will often be placed in areas of high economic value, the political costs of establishing and maintaining corridors will need to be assessed.

Finally, it is important to note that a longstanding debate among biologists and conservationists has been over the requisite dimensions of corridors. The appropriate minimum dimension of a corridor will, of course, depend on the species involved, and generally the smaller the target species, the smaller the corridor needed. As Dobson *et al.* (1999) point out, 'the home range requirements of carnivores, primates, and ungulates scales allometrically with body size'—which is to say that certain species will require extremely large corridors for effective movement.

The concept of corridors as a tool for conserving wildlife has now been adopted beyond the scientific community. Even the upper echelons of international policymaking on biodiversity has come around, as evinced by a 'Plan of Implementation' drafted under the auspices of the World Summit on Sustainable Development (WSSD) that includes the promotion 'of national and regional ecological networks and corridors' as a necessary step toward achieving the '2010 biodiversity target' (Bennett and Mulongey 2006). At its quadrennial Congress in 2008, the IUCN adopted a resolution on 'Enhancing ecological networks and connectivity conservation areas' that both 'requests states to establish national ecological networks and connectivity conservation areas to strengthen the protection of biodiversity, which include, as appropriate, biological corridors and buffer zones around protected areas,' and calls on states 'to strengthen the integration of biodiversity and ecological connectivity in terrestrial and marine planning, including conservation planning and especially actions on climate change mitigation and adaptation' (IUCN 2008). This decision was largely reiterated at the 2012 World Conservation Congress (IUCN 2012).

Today, a looming question for the science of corridor ecology is the relationship amongst corridors, protected areas, and the 'matrix'. With so much burgeoning work on and attention to corridors and connectivity, some conservation biologists have seen it necessary to reiterate one of the central tenets of conservation biology—viz., that protected areas are central to biodiversity conservation. As one prominent group of scientists emphasized: 'Conservation strategies that lack meaningful core areas are naïve, arrogant, and dangerous' (Noss *et al.* 1999). From this perspective, and in terms of the overall mission of biodiversity conservation, it is important to keep in mind that corridors are far more reliant on core areas than vice versa.

In contrast, others have argued that effective biodiversity conservation will require conservation biologists to pay closer attention to the matrix because opportunities to create new protected areas in many (if not most) places are extremely limited and most protected areas will never be large enough to conserve biodiversity in isolation from the surrounding lands. For example, in an extensive survey of the literature relevant to forest biodiversity conservation, Lindenmayer and Franklin (2002, 15) outlined the 'critical roles of the matrix for forest biodiversity,' and concluded that 'a conservation strategy based primarily or exclusively on reserves will fail because of its inherent limitations.' In some cases, they noted the matrix surrounding a protected area is compatible with conservation, thereby resulting in a *de facto* core area being much larger than the formally protected area itself. More recently, based largely on the extensive analysis by Prugh *et al.* (2008)

of ‘fragmented animal populations,’ Franklin and Lindenmayer (2009) have restated their case in stronger terms, arguing that the focus on core areas actually detracts from the imperative of protecting biodiversity throughout the matrix:

> Managers must realize that conservation of biological diversity is *not* primarily a set-aside issue that can be dealt with by reserving or modifying management on 10 or 20% of their landscape; rather, it is a pervasive issue that must be considered on every acre of land that they manage. Similarly, conservation scientists must reconsider the focus of their scientific endeavors if their goal is, truly, to retain the majority of the world’s biodiversity. For example, what key questions need to be empirically addressed to flesh out the matrix-based conservation biology paradigm? We also think some introspection by conservation scientists may be in order about why it has taken so long for academic conservation biology to recognize and accept the importance of matrix.

Hopefully, such words will not constitute a ‘shot across the bow’ that effectually reloads the cannons of an internecine battle reminiscent of the SLOSS debate. Standing for ‘single large or several small,’ this debate raged for many years within conservation circles over how to prioritize land conservation projects. The general consensus emerging from the debate was, to put it somewhat simplistically, that conservationists should aim to protect single large reserves *and* several small reserves—and pretty much anything else constituting viable habitat in rapidly changing landscapes (for an engaging description of both the science and personalities in this debate, see Quammen 1996, sections 127–157). Whatever the case, what is critical in our context is the recognition that corridors are inextricably woven into the matrix. As Lindenmayer and Franklin (2002, 34) originally put it, assessing the efficacy of corridors for connectivity ‘cannot be made without consideration of the matrix . . . if there is continued habitat loss in the surrounding matrix, the establishment of corridors may make only a limited contribution to biodiversity conservation.’

CLIMATE CHANGE IN THE MOUNTAINS

Several studies indicate that ‘high elevation environments . . . are among the most sensitive to climatic changes occurring on a global scale’ (Diaz *et al.* 2003, 2). Pounds *et al.* (2006) articulate this ‘prevailing idea’ that extinction risks are greater for higher elevation species inasmuch that: ‘Many are already prone to extinction, because geographic ranges tend to decrease in size with increasing elevation. The probability of disappearance might thus be expected to increase from lowlands to mountain tops.’ Dating back to the 1950s (see Körner 2000), scientific research on climate change in the mountains gives weight to this concern, and several noteworthy studies are highlighted here (although it is important to note that the following is hardly exhaustive).

Many researchers have examined the relationship between climate change and vegetative changes in mountain ecosystems. For example, in the 1990s, a widely recognized study from the Alps found that 'there is no doubt that even moderate warming induces migration processes, and that this process is underway.' Based on extensive time-series evidence of plant responses to climate change, the analysis reached the conclusion that climate change 'may cause disastrous extinctions in these environments' (Grabherr *et al.* 1994). Scientists have since undertaken a sizable number of empirical and modelling investigations on the effects of climate change on mountain vegetation; while there remains high uncertainty over the relationship between climate and other factors (such as soil substrate, human use, and animal/livestock impacts), no few studies have detected discernible influence of climate change on mountain vegetation (see, for instance: Dullinger *et al.* 2012; Gottfried *et al.* 2012; Krishnaswamy *et al.* 2014; Rustad *et al.* 2012; and Svenning and Sandel 2013).

In 1995, the International Panel on Climate Change included an extensive review of the effect of climate change on mountain systems in its Second Assessment Report (IPCC 1995, Chapter 5). The IPCC's summary of this review succinctly pulls together the essential points on how climate change is expected to affect mountain regions:

> The projected decrease in the extent of mountain glaciers, permafrost and snow cover caused by a warmer climate will affect hydrologic systems, soil stability and related socioeconomic systems. The altitudinal distribution of vegetation is projected to shift to higher elevation; some species with climatic ranges limited to mountain tops could become extinct because of disappearance of habitat or reduced migration potential. Mountain resources such as food and fuel for indigenous populations may be disrupted in many developing countries. Recreational industries—of increasing economic importance to many regions—also are likely to be disrupted (IPCC 1996, 7).

Over the subsequent decade, research on climate change in mountain regions has not significantly changed this basic assessment; to pull but one recent example of a continent-scale analysis of snow pack trends, Pederson *et al.* (2011) find that the 'increasing role of warming on large-scale snowpack variability and trends foreshadows fundamental impacts on streamflow and water supplies across the western USA.' Such consistent findings may partially explain why the IPCC's Third Assessment Report (TAR) in 2001 and Fourth Assessment Report (AR4) in 2007 did not contain a chapter specific to mountain regions. However, the TAR does include extensive coverage and analysis of the worldwide phenomenon of glacial retreat, and a subsection on ecosystem services points out that conforming with general climatic trends, climate change is likely to have a greater effect on mountain regions at higher latitudes (IPCC 2001). In 2007, the AR4 noted that since 2001, 'the literature has confirmed a disproportionately high risk of extinction for many endemic species in various mountain ecosystems' (IPCC 2007, 232).

A recent modeling exercise on the effects of climate change on mountain biodiversity (viz., 'simulated species' and the world's 1,009 montane bird species) under various dispersal parameters found that after arctic ecosystems, 'there is probably no other terrestrial global biological system that is more extensively and demonstrably threatened by impending climate change, and no other that offers fewer excuses for scientific or conservation inaction' (La Sorte and Jetz 2010). Other studies have found that the threat posed by climate change appears to be particularly strong for montane cloud forests due to the combined phenomena of reduced cloud contact and increased evapo-transpiration, both of which 'could have serious conservation implications, given that these ecosystems typically harbor a high proportion of endemic species and are often situated on mountain tops or ridge lines' (see also Bruijnzeel *et al.* 2010; Still *et al.* 1999, 608). These concerns have been corroborated in a number of still more recent studies (e.g., Chen *et al.* 2011; Dirnböck *et al.* 2011; Engler *et al.* 2011; Forero-Medina *et al.* 2011a, 2011b; Ponce-Reyes *et al.* 2013; Proctor *et al.* 2011). Although this literature is vast and continues to grow, it is worth noting that one of the more well-noted studies was by Pounds *et al.* (1999), who found that population crashes of twenty anuran species (frogs and toads) in the Monteverde highland forests of Costa Rica 'probably belong to a constellation of demographic changes that have altered communities of birds, reptiles and amphibians in the area and are linked to recent warming' (p. 611). These findings generated a fairly heated debate (for a review see McMenamin *et al.* 2011), one that continues to this day over the ability to attribute the decline of an individual species to climate change see Venesky *et al.* 2013 for a recent agnostic overview of current thinking on climate change and amphibian declines; for a more general discussion of attribution, see Parmesan *et al.* 2011).

Yet even as climate change in the mountains poses a considerable threat to biodiversity, it is important to take into account both the 'mitigating circumstances' as well as the complex responses that montane and alpine species will maintain in the face of climate change. For example, not all mountain species will be affected by climate change; some species have even been shown to remain in the same mountain sites despite thousands of years of 'natural' climate changes. Furthermore, it is important to note that although climate change is likely to be a particular threat to species living in alpine zones, mountains are also potentially capable of affording greater habitat flexibility to many mountain species. Some evidence, for example, points to bird species in mountains as being more likely to withstand climate change than bird species on the plains (Peterson 2003). A number of factors play into this, including the facts (1) that in level areas the nearest climate envelope is potentially much further away than in topographically diverse mountain regions, and (2) that slope, aspect, elevation, and north–south gradients offer a multitude of options for birds to find a climate optimum as well as an ideal niche space. Another consideration, put forth in the IPCC's TAR, is that 'direct human impacts on alpine vegetation from grazing, tourism, and nitrogen deposition are so strong that climatic effects on the goods and services provided by alpine ecosystems are difficult to detect' (Gitay *et al.* 2001, 241; see also Körner 2000; note, however, that a recent initiative in Australia has found that altitudinal shifts can be accurately measured through statistical sampling techniques that focus on mean altitudinal range rather than range boundaries; see Shoo *et al.* 2006). It is also worth noting that the 2002 UN designation as 'Year of the Mountains' led to an extensive research effort, much of it encapsulated in the extensive compilation, *Global Change and Mountain Regions: An Overview of Current Knowledge* (Huber *et al.* 2005). While the volume in general demonstrates the magnitude of global change in mountain ecosystems, the lead analysis on vegetative change emphasizes that: 'Evidence accumulated over the past years suggests that there is no common biotic response to any of these environmental drivers but rather a series of context-driven responses with each of these three atmospheric changes [T°, CO_2, nitrogen deposition] exerting different effects on different plant species and in different vegetation' (Körner 2005).

Taking into account these caveats, climate change nonetheless remains a tremendous threat to mountain biodiversity. Perhaps the greatest threat is that of 'rapid climate change' or 'abrupt climate change,' entailing a pace of environmental change under which many plant species would simply be unable to spread to higher elevations—if indeed, they could survive the presumably harsher annual temperature variations at such altitudes (for three different perspectives on rapid or abrupt climate change, see Bradshaw and Holzapfel 2006; Charlesworth and Okereke 2010; Clark 2010). In such a bleak scenario, if a plant species were not able to spread to higher elevation, different aspects, or more northerly latitudes, the end result could well be widespread extirpation and even extinction.

In a recent meta-analysis of 'rapid range shifts of species associated with high levels of climate warming,' Chen *et al.* (2011) found that for a range of taxonomic groups in Europe, North America, Malaysia, and Marion Island, species ranges had gained in elevation a median 11 meters per decade (the study also examined latitudinal range shifts, with similar results). This shift implied 'much greater responses of species to climate warming than previously reported.'

MOUNTAIN CORRIDORS: A SOLUTION TO CLIMATE CHANGE?

Can corridors provide a 'solution' to the problem of climate change in mountain systems? This is hardly an original notion. By 1991, Hobbs and Hopkins (1991, 282) were able to generalize that: 'One commonly touted solution to the problems of habitat fragmentation in the face of greenhouse-driven climatic change is to establish corridors to provide for migration.' And a year later, in the first major volume dedicated to the effects of global warming on biodiversity, Peters (1992, 24) argued that: 'Corridors along altitudinal gradients are likely to be most practical because they can be relatively short compared with the longer distances necessary to accommodate latitudinal shifting.' Hamilton (1997, 63) pointed out the vulnerability of single mountain protected areas as sky islands, and advocated for altitudinal corridors as well as for bioregional conservation corridors along mountain ranges running both poleward and latitudinally. Since these early publications, discussions of climate change and corridors have been intimately linked. More recently, an extensive review of the literature on biodiversity and climate change indicated that maintaining connectivity and corridors is the most commonly recommended means to help species and ecosystems adapt to climate change (Heller and Zavaleta 2009; also see Mawdsley *et al.* 2009). Yet with increasing recognition of the importance of connectivity in biodiversity conservation, Kostyack *et al.* (2011) make the important point that connectivity will likely be 'necessary but insufficient for preventing climate-induced extinctions' and thereby necessitate a number of additional conservation policies.

One widely noted 'on the ground' example of the relationship between connectivity and climate change can be found under the banner of 'Yellowstone to Yukon' (Y2Y), a very large undertaking at 1.3 million square kilometers, or about three times the extent of California (Chester 2006). When the Executive Director of Y2Y's organizational hub (the 'Y2Y Conservation Initiative') was asked what Y2Y planned to do about the challenge of climate change, his immediate response was that 'Y2Y *is* a response to climate change.' His point goes straight to the basic premise within the conservation community already discussed—viz., that the best response to climate change is to give biodiversity *the ability to move* in accordance with changing habitat conditions. From this standpoint, it is hardly a long stretch to the idea that corridors present us with a promising method for enabling such movement.

First conceived in 1993, Y2Y is many things: a transboundary region, a vision for the landscape, a network of hundreds of NGOs and individuals, and a 'not-for-profit organization that seeks to preserve and maintain the wildlife, native plants, wilderness and natural processes of the mountainous region from Yellowstone National Park to the Yukon Territory' (Locke 2010). A fundamental goal of Y2Y is to ensure that the vast mountain landscape in the northwestern quarter of North America carries sufficient biological connectivity to protect biodiversity in the long-term. While conservationists working under the aegis of Y2Y have long been cognizant of the threat of climate change to the region, the principal focus has been to bring a halt to—or at least slow down—the rate of habitat loss and degradation due to various forms of anthropogenic development pressures. Yet they are also coming to recognize that the looming problem of climate change could become as equally severe an obstacle to effective biodiversity conservation in mountain regions (Graumlich and Biennen 2010).

Unfortunately, the proposition that connectivity is the key to climate change adaptation remains largely untested, and there is little empirical evidence either way over whether mountain corridors can ultimately protect biodiversity from the effects of climate change (Chester and Hilty 2010). Yet as Hilty *et al.* (2006, 112) summarize in general terms, 'it is hard to imagine any realistic alternative that would be conducive to species persistence.' To some degree, species translocaton (also described as assisted colonization, assisted migration, and managed relocation) has garnered increasing support from biologists studying the effects of climate change (see Thomas 2011). Yet translocation is an exceptionally costly task, one that entails not negligible risks. Other response options, including genetic manipulation and controlling greenhouse gas emissions, seem outlandishly dangerous or politically unpalatable. In comparison, corridors appear to be our best comparatively reasonable hope for protecting mountain biodiversity in the long-term.

CONCLUSION

In the pursuit of biodiversity conservation throughout the world's mountain regions, collaboration will be critical amongst three largely disparate scientific research communities: the mountain research community, the corridor ecology community, and the climate change community. What makes this congruence critical? To a large extent, the answer revolves around the two most familiar drivers of biodiversity loss: habitat destruction and habitat fragmentation. Some conservationists still unfortunately consider climate change as, for lack of a better term, simply one of numerous 'independent variables' acting on species survival. Yet it is of fundamental importance that climate change be seen more as an exacerbating force over the panoply of direct human alterations to mountain landscapes. Indeed, both because climate change has an additive or perhaps even a multiplicative effect on other threats to biodiversity, and because montane regions are experiencing a stronger impact of climate change, the three disciplines need to work together to ensure the resilience of mountain ecosystems.

While there are many ways to go about 'fixing' the problem of habitat destruction and fragmentation, we echo the many calls for a "climate smart," "climate-ready," or "climate savvy" approach (Hansen *et al.* 2010; Hansen & Hoffman 2011; Hilty *et al.* 2012) to ountain biodiversity conservation; one that will allow us to dramatically better communicate without ignoring the diversity within the global community of mountain scientists and conservationists. This approach begins with four questions emanating from the three scientific communities we have described. These are, respectively:

1. What do we need to know about mountain biodiversity and how does it interact with human communities in the mountains?
2. Given what we know in response to the first question, can we accept the premise that corridors provide sufficient connectivity between 'natural' communities, species, and their populations in mountain regions?
3. Even if we craft accurate and useful responses to questions 1 and 2, to what degree will anthropogenic climate change require modification of those responses?
4. How can we best build resilience into mountain ecosystems?

Although not comprehensive, these four questions encapsulate a unified mountain research agenda. As we strive to answer—and then to continuously reframe both those questions and answers—these three research communities will enhance our capacity to implement adaptive management and to foster those components of the human and biological landscapes that provide resilience (Gunderson and Folke 2005; see also Peterson *et al.* 1997a and Tschakert and Dietrich 2010). And in our attempts to implement a conservation agenda, we must keep in mind two potential pitfalls. The first may sound hackneyed, but deserves emphasis: our community—or rather, communities—must allow for and encourage interdisciplinary approaches. In short, although answering each one of the above questions constitutes an integral component to achieving biodiversity conservation, answering any of them in isolation will likely steer us down unproductive paths.

Second, each question is decidedly broad, and significant controversies will undoubtedly arise within and among our converging disciplines. It will take a tremendous force of will—mixed with strong doses of diplomacy and open-mindedness—to ensure that we are tolerant of the opinions of others *while at the same time* we collectively maintain a focus on the fundamental mission of conserving the world's mountain biodiversity. There is hardly a guarantee that we will succeed. But if the community of people who care about mountain biodiversity can accomplish these 'ground level' tasks, we may then be in a position to protect the full diverse range of mountain life.

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REFERENCES

Adirondack Council (1998) *Acid rain: A continuing national tragedy*. Elizabethtown, NY.

Anderson, A.B. and Jenkins, C.N. (2006) *Applying nature's design: Corridors as a strategy for biodiversity conservation*. New York: Columbia University Press.

Ariza C., Maselli, D., and Kohler, T. (2013) *Mountains: Our life, our future. Progress and perspectives on sustainable mountain development from Rio 1992 to Rio 2012 and beyond*. Bern: Swiss Agency for Development and Cooperation and Centre for Development and Environment.

Beever, E.A., Ray, C., Mote, P.W. and Wilkening, J.L. (2010) Testing alternative models of climate-mediated extirpations. *Ecological Applications* 20(1): 164–178.

Beier, P. and. Noss, R.F. (1998) Do habitat corridors provide connectivity? *Conservation Biology* 12(6): 1241–1252.

Bennett, A.F. (2003) *Linkages in the landscape: The role of corridors and connectivity in wildlife conservation*. Gland, Switzerland: IUCN.

Bennett, G. (1994) *Conserving Europe's natural heritage: Towards a European ecological network*. London: Graham and Trotman Limited.

Bennett, G. and Mulongoy, K.J. (2006) *Review of experience with ecological networks, corridors and buffer zones*. Montreal: Secretariat of the Convention on Biological Diversity. Technical Series No. 23.

Berger, J. (2004) The last mile: How to sustain long-distance migration in mammals. *Conservation Biology* 18(2): 320–331.

Bernbaum, E. (1990) *Sacred mountains of the world*. San Francisco: Sierra Club Books.

—— (1997) The spiritual and cultural significance of mountains. In B. Messerli and J.D. Ives (eds), *Mountains of the world: A global priority*. New York: Parthenon Publishing Group, pp. 39–60.

—— (1998) *Sacred Mountains of the World*. Los Angeles: University of California Press.

Bona, F., Badino, G. and Isaia, M. (2006) Designing a "tailor-made" ecological network using geographical information systems. *Ecological Research* 21(4): 605–610.

Bradshaw, W.E. and Holzapfel, C.M. (2006) Evolutionary response to rapid climate change. *Science* 312(5779): 1477–1478.

Bruijnzeel, L.A., Scatena, F.N. and Hamilton, L.S. (2010) *Tropical montane cloud forests: Science for conservation and management*. Cambridge: Cambridge University Press.

Chape, S., Spalding, M. and Jenkins, M. (2008) *The world's protected areas: Status, values and prospects in the 21st century*. Berkeley, CA: University of California Press.

Chapin, M. (2004) A challenge to conservationists. *Worldwatch*. November/December: 17–31.

Charlesworth, M. and Okereke, C. (2010) Policy responses to rapid climate change: An epistemological critique of dominant approaches. *Global Environmental Change* 20(1): 121–129.

Chen, C., Hill, J.K., Ohlemüller, R., Roy, D.B. and Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024–1026.

Chester, C.C. (2006) *Conservation across borders: Biodiversity in an interdependent world*. Washington, D.C.: Island Press.

Chester, C.C. and Hilty, J.A. (2010) Connectivity science. In G.L. Worboys, W.L. Francis and M. Lockwood (eds), *Connectivity conservation management: A global guide*. London: Earthscan, pp. 22–33.

Chetkiewicz, C.-L.B., St. Clair, C.C. and Boyce, M.S. (2006) Corridors for conservation: Integrating pattern and process. *Annual Review of Ecology, Evolution, and Systematics* 37(1): 317–342.

Clark, N. (2010) Volatile worlds, vulnerable bodies. *Theory, Culture & Society* 27(2–3): 31–53.

Crooks, K. and Sanjayan, M. (eds) (2006) *Connectivity conservation*. Cambridge: Cambridge University Press.

Damschen, E.I., Haddad, N.M., Orrock, J.L., Tewksbury, J.J. and Levey, D.J. (2006) Corridors increase plant species richness at large scales. *Science* 313(5791): 1284–1286.

Diaz, H.F., Grosjean, M. and Graumlich, L. (2003) Climate variability and change in high elevation regions: Past, present and future. *Climatic Change* 59(1): 1–4.

Dirnböck, T., Essl, F. and Rabitsch, W. (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology* 17:(2): 990–996.

Dobrowski, S.Z. (2011) A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology* 17(2): 1022–1035.

Dobson, A., Ralls, K., Foster, M., Soule, M.E., Simberloff, D., Doak, D., Estes, J.A., Mills, L.S., Mattson, D., Dirzo, R., Arita, H., Ryan, S., Norse, E.A., Noss, R.F. and Johns, D. (1999) Connectivity: Maintaining flows in fragmented landscapes. In Michael E. Soulé and John Terborgh (eds), *Continental conservation: Scientific foundations of regional reserve networks*. Washington: Island Press, pp. 129–170.

Doerr, V.A.J., Barrett, T. and Doerr, E.D. (2011) Connectivity, dispersal behaviour and conservation under climate change: A response to Hodgson *et al*. *Journal of Applied Ecology* 48(1): 143–147.

Engler, R., Randin, C.F., Thuiller, W., Dullinger, S., Zimmermann, N.E., Araújo, M.B., Pearman, P.M., Le Lay, G., Piedallu, C., Albert, C.H., Choler, P., Coldea, G., De Lamo, X., Dirnböck, T., Gégout, J.-C., Gómez-García, D., Grytnes, J.A., Heegaard, E., Holstad, F., Nogués-Bravo, D., Normand, S., Puscas, M., Sebastiá, M.T., Stanisci, A., Theurillat, J.P., Trivedi, M.R., Vittoz, P. and Guisan, A. (2011) 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology* 17(7): 2330–2341.

Epps, C.W., Palsboll, P.J., Wehausen, J.D., Roderick, G.K., Ramey, R.R. and McCullough, D.R. (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters* 8(10): 1029–1038.

Forero-Medina, G., Joppa, L. and Pimm, S.L. (2011) Constraints to species' elevational range shifts as climate changes. *Conservation Biology* 25(1): 163–171.

Forero-Medina, G., Terborgh, J., Socolar, S.J. and Pimm, S.L. (2011) Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS ONE* 6(12): e28535.

Forman, R.T.T. (1991) Landscape corridors: From theoretical foundations to public policy. In Denis A. Saunders and R. J. Hobbs (eds), *Nature conservation 2: The role of corridors*. Chipping Norton, NSW, Australia: Surrey Beatty.

—— (1995) *Land mosaics: The ecology of landscapes and regions*. New York: Cambridge University Press.

Franklin, J.F. and Lindenmayer, D.B. (2009) Importance of matrix habitats in maintaining biological diversity. *Proceedings of the National Academy of Sciences* 106(2): 349–350.

Gilbert-Norton, L., Wilson, R., Stevens, J.R. and Beard, K.H. (2010) A meta-analytic review of corridor effectiveness. *Conservation Biology* 24(3): 660–668.

Gitay, H., Brown, S., Easterling, W. and Jallow, B. (2001) Ecosystems and their goods and services. In J.J. McCarthy, J.J. Canziani, O.F. Leary, D.J. N.A. Dokken and K.S. White (eds), *Climate change 2001: Impacts, adaptation, and vulnerability: Contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, pp. 237–342.

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J.L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M.a.R., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moissev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I., Grabherr, G. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change* 2, 111–115.

Grabherr, G., Gottfried, M. and Pauli, H. (1994) Climate effects on mountain plants. *Nature* 369(6480): 448.

Graumlich, L., Bienen, L. (2010) *Moving toward climate change adaptation: The promise of the Yellowstone to Yukon Conservation Initiative for addressing the region's vulnerabilities*. Yellowstone to Yukon Conservation Initiative, Canmore, Alberta.

Gunderson, L. and Folke, C. (2005) Resilience: Now more than ever. *Ecology and Society* 10(2).

Haddad, N.M., Hudgens, B., Damschen, E.I., Levey, D.J., Orrock, J.L., Tewksbury, J.J. and Weldon, A.J. (2011) Assessing positive and negative ecological effects of corridors. In J. Liu, V. Hull, A.T. Morzillo and J.A. Wiens (eds), *Sources, Sinks and Sustainability across landscapes*. Cambridge: Cambridge University Press, pp. 475–506.

Hamilton, L. S. (2006) Protected areas in mountains. *Pirineos* 161: 151–158.

Hamilton, L., Askew, B. and Odell, A. (1982) *Forest History*. Albany, NY: New York State Department of Environmental Conservation. New York State Forest Resources Assessment Report No.1.

Hamilton, L. and McMillan, L. (eds) (2004) *Guidelines for planning and managing mountain protected areas*. Gland, Switzerland: IUCN.

Hamilton, L.S. (1996) The role of protected areas in sustainable mountain development. *Parks* 6(1): 2–13.

—— (1997) Mountain ecoregions in mountain conservation corridors. *Wild Earth* 7(2): 63–66.
—— (1999) Enlarging and linking Andean protected areas into corridors. In F. Sarmiento and J. Hidalgo (eds), *III International Symposium on sustainable mountain development: Understanding ecological interfaces of Andean cultural landscapes for management*. Quito: Andean Mountain Association & Panamerican Center for Geographical Studies and Research, pp. 65–70.
Hamilton, L.S., Juvik, J.O. and Scatena, F.N. (1995) *Tropical montane cloud forests*. New York: Springer-Verlag.
Hansen, A.J., Rasker, R., Maxwell, B., Rotella, J.J., Johnson, J.D., Parmenter, A.W., Langner, U., Cohen, W.B., Lawrence, R.L. and Kraska, M.P.V. (2002) Ecological causes and consequences of demographic change in the new west *BioScience* 52,(2): 151–162.
Hansen, L., Hoffman, J., Drews, C. and Mielbrecht, E. (2010) Designing climate-smart conservation: Guidance and cases studies. *Conservation Biology* 24, 63–69.
Hansen, L.J and Hoffman, J.R. (2011) *Climate savvy: Adapting conservation and resource management to a changing world*. Washington, DC: Island Press.
Hanski, I. (1998) Metapopulation dynamics. *Nature* 396: 41–49.
Harmon, D. and Worboys, G. (eds) (2004) *Managing mountain protected areas: Challenges and responses for the 21st century*: Gland, Switzerland: INCN.
Harris, L.D. (1984) *The fragmented forest: Island biogeography theory and the preservation of biotic diversity*. Chicago: University of Chicago Press.
Harris, L.D. and Scheck, J. (1991) From implications to applications: The dispersal corridor principle applied to the conservation of biological diversity. In D.A. Saunders and R.J. Hobbs (eds), *Nature conservation 2: The role of corridors*. Chipping Norton, Australia: Surrey Beatty, pp. .189–220.
Heller, N.E. and Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation* 142(1): 14–32.
Hilty, J.A., Chester, C.C. and Cross, M.S. (2012) *Climate and conservation: Landscape and seascape science, planning, and action*. Washington, DC: Island Press.
Hilty, J.A., Lidicker, W.Z. and Merenlender, A.M. (2006) *Corridor ecology: The science and practice of linking landscapes for biodiversity conservation*. Washington, DC: Island Press.
Hobbs, R.J. and Hopkins, A.J.M. (1991) The role of conservation corridors in a changing climate. In D.A. Saunders and R.J. Hobbs (eds), *Nature conservation 2: The role of corridors*. Chipping Norton, Australia: Surrey Beatty, pp. 281-290.
Hodgson, J.A., Thomas, C.D., Wintle, B.A. and Moilanen, A. (2009) Climate change, connectivity and conservation decision making: Back to basics. *Journal of Applied Ecology* 46(5): 964-969.
Huber, U.M., Bugmann, H.K.M. and Reasoner, M.A. (eds) (2005) *Global change and mountain regions: An overview of current knowledge*. Dordrecht, The Netherlands: Springer.
Hudson, W.E. (ed.) (1991) *Landscape linkages and biodiversity*. Washington, DC: Island Press for Defenders of Wildlife.
Imbrie, J. and Imbrie, K.P. (1979) *Ice ages: Solving the mystery*. Short Hills, NJ: Enslow Publishers.
IPCC (1995) *Climate Change 1995: The science of climate change*. Intergovernmental Panel on Climate Change. Summary for Policymakers and Technincal Summary of the Working Group I Report.
—— (1996) *Summary for policymakers: Scientific-technical analyses of impacts, adapta-*

tions and mitigation of climate change. Working Group II, Intergovernmental Panel on Climate Change. http://www.ipcc.ch/pub/sarsum2.htm.

—— (2001) *Climate Change 2001: Synthesis Report: Summary for Policymakers*. Intergovernmental Panel on Climate Change. http://www.ipcc.ch/pub/un/syreng/spm.pdf.

—— (2007) *Climate Change 2007: Impacts, adaptation and vulnerability*. Cambridge: Cambridge University Press. Contribution of Working Group II to the fourth assessment report of the Intergovernmental Panel on Climate Change. http://www.ipcc.ch/ipccreports/ar4-wg2.htm

IUCN (1997) *Resolutions and recommendations: World Conservation Congress, Montreal, Canada, 13–23 October 1996*. Gland, Switzerland: IUCNO.

—— (2008) *Resolution 4.062: Enhancing ecological networks and connectivity conservation areas*. Gland, Switzerland: IUCN.

—— (2012) *Resolution 056: Enhancing connectivity conservation through international networking of best practice management*. Gland, Switzerland: IUCN.

Ives, J.D. (1973) Preface. *Arctic and Alpine Research* 5(3): A–A2.

—— and Messerli, B. (1989) *The Himalayan dilemma: Reconciling development and conservation*. New York: Routledge for United Nations University.

—— (1990) Progress in theoretical and applied mountain research, 1973–1989, and major future needs. *Mountain Research and Development* 10(2): 101–127.

—— and Spiess, E. (1997) Mountains of the world: A global priority. In B. Messerli and J.D. Ives (eds), *Mountains of the world: A global priority*. New York: Parthenon Publishing Group, pp. 1–15.

Jenkins, J., Roy, K. and Driscoll, C. (2007) *Acid rain in the Adirondacks: An environmental history*. Ithaca, NY: Comstock Pub. Associates/Cornell University Press.

Kapos, V., Rhind, J., Edwards, M., Price, M.F. and Ravilious, C. (2000) Developing a map of the world's mountain forests. In M.F. Price and N. Butt (eds), *Forests in sustainable mountain development: A state of knowledge report for 2000*. New York: CABI Pub. in association with the International Union of Forestry Research Organizations.

Körner, C. (2000) The alpine life zone under global change. *Gayana Botanica* 5(1).

—— (2005) The green cover of mountains in a changing environment. In U.M. Huber, H.K.M. Bugmann and M.A. Reasoner (eds), *Global change and mountain regions: An overview of current knowledge*. Dordrecht, The Netherlands: Springer, pp. 367–375.

Körner, C. and Spehn, E.M. (2002) *Mountain biodiversity: A global assessment*. Boca Raton, FL: Parthenon Pub. Group.

Kostyack, J., Lawler, J.J., Goble, D.D., Olden, J.D. and Scott, J.M. (2011) Beyond reserves and corridors: Policy solutions to facilitate the movement of plants and animals in a changing climate. *BioScience* 61(9): 713–719.

Krishnaswamy, J., John, R., and Joseph, S. (2014) Consistent response of vegetation dynamics to recent climate change in tropical mountain regions. *Global Change Biology* 20, 203–215.

La Sorte, F.A. and Jetz, W. (2010) Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences* 277(1699): 3401–3410.

Lauer, W. (ed.) (1984) *Natural environment and man in tropical mountain ecosystems: Proceedings of the symposium of the Akademie der Wissenschaften und der Literatur, Mainz, Kommission für Erdwissenschaftliche Forschung, in connection with the International Geographical Union, Commission on Mountain Geoecology, February 24–26, 1983 at Mainz*. Wiesbaden: F. Steiner Verlag.

Lavergne, S., Thuiller, W., Molina, J. and Debussche, M. (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: A 115-year study in the Mediterranean region. *Journal of Biogeography* 32(5): 799–811.

Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., Bertzky, B., Butchart, S.H.M., Stuart, S.N., Badman, T., Rodrigues, A.S.L. 2013. Protected areas and effective biodiversity conservation. *Science* 342: 803–805.

Lindenmayer, D. and Franklin, J.F. (2002) *Conserving forest biodiversity: A comprehensive multiscaled approach*. Washington, D.C.: Island Press.

Locke, H. (2010). Yellowstone to Yukon connectivity conservation. In G.L. Worboys, W.L. Francis and M. Lockwood (eds), *Connectivity conservation management: A global guide*. London: Earthscan, pp. 161–181.

Lowenthal, D. (2000). *George Perkins Marsh, prophet of conservation*. Seattle, WA: University of Washington Press.

MacArthur, R.H. and Wilson, E.O. (1967) *The theory of island biogeography*. Princeton, NJ: Princeton University Press.

Manuel-Navarrete, D., Slocombe, S. and Mitchell, B. (2006) Science for place-based socio-ecological management: Lessons from the Maya Forest (Chiapas and Petén). *Ecology and Society* 11(1): Article 28.

Marsh, G.P. (1864 [1965]) *Man and nature: Or, physical geography as modified by human action*. Cambridge, Massachusetts: Belknap Press of Harvard University Press.

Mawdsley, J.R., O'Malley, R. and Ojima, D.S. (2009) A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology* 23(5): 1080–1089.

McKelvey, K.S., Copeland, J.P., Schwartz, M.K., Littell, J.S., Aubry, K.B., Squires, J.R., Parks, S.A., Elsner, M.M. and Mauger, G.S. (2011). Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications* 21(8): 2882–2897.

McMenamin, S.K. and Hannah, L. (2011) First extinctions on land. In L. Hannah (ed.), *Saving a million species: Extinction risk from climate change*. Washington, DC: Island Press, pp. 89–101.

Messerli, B. and Ives, J.D. (eds) (1997) *Mountains of the world: A global priority*. New York: Parthenon Publishing Group.

Millar, C.I. and Westfall, R.D. (2010) Distribution and climatic relationships of the American pika (*Ochotona princeps*) in the Sierra Nevada and Western Great Basin, USA; Periglacial landforms as refugia in warming climates. *Arctic, Antarctic, and Alpine Research* 42(1): 76–88.

Mountain Agenda (1992) *An Appeal for the Mountains*. Berne, Switzerland: University of Berne.

Nicolson, M.H. (1959) *Mountain gloom and mountain glory: The development of the aesthetics of the infinite*. Seattle, WA: University of Washington Press (1997 edition).

Noss, R.F. (1994) The Wildlands Project: Land conservation strategy. In R.E. Grumbine (ed.), *Environmental policy and biodiversity*. Washington, DC: Island Press, pp. 233–266.

Noss, R.F., Dinerstein, E., Gilbert, B., Gilpin, M., Miller, B.J., Terborgh, J. and Trombulak, S. (1999) Core Areas: Where Nature Reigns. In M.E. Soulé and J. Terborgh (eds), *Continental Conservation: Scientific Foundations of Regional Reserve Networks*. Washington, DC: Island Press, pp. 99–128.

Parmesan, C., Duarte, C., Poloczanska, E., Richardson, A.J. and Singer, M.C. (2011) Overstretching attribution. *Nature Climate Change* 1: 2–4.

Pederson, G.T., Gray, S.T., Woodhouse, C.A., Betancourt, J.L., Fagre, D.B., Littell, J.S., Watson, E., Luckman, B.H. and Graumlich, L.J. (2011) The unusual nature of recent snowpack declines in the North American cordillera. *Science* 333: 332–335.

Peters, R.L. (1992) Conservation of biological diversity in the face of climate change. In R.L. Peters and T.E. Lovejoy (eds), *Global Warming and Biodiversity*. New Haven, CT: Yale University Press, pp. 15–30.

Peterson, A.T. (2003) Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. *Global Change Biology* 9(5): 647–655.

Peterson, G., De Leo, G.A., Janssen, M.A., Hellmann, J.J., Kinzig, A., Malcolm, J.R., O'Brien, K.L., Pope, S.E., Rothman, D.S., Shevliakova, E. and Tinch, R.R.T. (1997) Uncertainty, climate change, and adaptive management. *Ecology and Society [Conservation Ecology]* 1(2).

Ponce-Reyes, R., Nicholson, E., Baxter, P.W.J., Fuller, R.A., Possingham, H. (2013) Extinction risk in cloud forest fragments under climate change and habitat loss. *Diversity and Distributions* 19: 518–529.

Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S. and Pulliam, H.R. (2001) Making Smart Conservation Decisions. In M.E. Soulé and G.H. Orians (eds), *Conservation biology: Research priorities for the next decade*. Washington, D.C.: Island Press, pp. 225–244.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sanchez-Azofeifa, G.A., Still, C.J. and Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439(7073): 161–167.

Pounds, J.A., Fogden, M.P.L. and Campbell, J.H. (1999) Biological response to climate change on a tropical mountain. *Nature* 398: 611–615.

Price, M.F. (1999) *Global change in the mountains: Proceedings of the European Conference on Environmental and Societal Change in Mountain Regions, Oxford, UK, 18–20 December 1997*. Parthenon Publishing Group, New York.

—— (2011) The Centre for Mountain Studies. *Mountain Research and Development* 31: 166–168.

——, Byers, A.C., Friend, D.A., Kohler, T., Price, L.W. (2013) *Mountain geography: Physical and human dimensions*. Berkeley: University of California Press.

Proctor, M.F., Paetkau, D., McLellan, B.N., Stenhouse, G.B., Kendall, K.C., Mace, R.D., Kasworm, W.F., Servheen, C., Lausen, C.L., Gibeau, M.L., Wakkinen, W.L., Haroldson, M.A., Mowat, G., Apps, C.D., Ciarniello, L.M., Barclay, R.M.R., Boyce, M.S., Schwartz, C.C. and Strobeck, C. (2012) Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monographs* 180(1).

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E and Brashares, J.S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences* 105(52): 20770–20775.

Purchase, E. (1999). *Out of nowhere: Disaster and tourism in the White Mountains*. Baltimore, MD: Johns Hopkins University Press.

Quammen, D. (1996) *The song of the dodo: Island biogeography in an age of extinctions*. New York: Scribner.

Romano, B. and Zullo, F. (2012) Landscape fragmentation in Italy: Indices implementation to support territorial policies. In: M. Campagna, A. De Montis, F. Isola, S. Lai,

C. Pira and C. Zoppi (eds), *Planning support tools: Policy analysis/implementation and evaluation*. Milan: FrancoAngelica, pp. 399–414.

Ray, C., Beever, E. and Loarie, S. (2012) Retreat of the American pika: Up the mountain or into the void? In J.F. Brodie, E.S. Post and D.F. Doak (eds), *Wildlife conservation in a changing climate*. Chicago: The University of Chicago Press, pp. 245–270.

Rodríguez-Rodríguez, D., Bomhard, B., Butchart, S.H.M. and Foster, M.N. (2011) Progress towards international targets for protected area coverage in mountains: A multi-scale assessment. *Biological Conservation* 144(12): 2978–2983.

Rosenberg, D.K., Noon, B.R. and Meslow, E.C. (1997) Biological corridors: Form, function, and efficacy. *BioScience* 47(10): 677–687.

Runte, A. (1987) *National parks: The American experience*, 2nd edn. Lincoln, NE: University of Nebraska Press.

Rustad, L., Campbell, J., Dukes, J.S., Huntington, T., Lambert, K.F., Mohan, J. and Rodenhouse, N. (2012) *Changing climate, changing forests: The impacts of climate change on forests of the northeastern United States and eastern Canada*. U.S. Forest Service, Newtown Square, Pennsylvania.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. and Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience* 52(10): 891–904.

Saunders, D.A. and Hobbs, R.J. (eds) (1991) *Nature conservation 2: The role of corridors*. Chipping Norton, Australia: Surrey Beatty.

Schneider, P. (1997) *The Adirondacks: A history of America's first wilderness*, 1st edn. New York: H. Holt and Co.

Scott, J.M., Davis, F.W., McGhie, R.G., Wright, R.G., Groves, C. and Estes, J. (2001) Nature reserves: Do they capture the full range of America's biological diversity? *Ecological Applications* 11(4): 999–1007.

Shoo, L.P., Williams, S.E. and Hero, J.-M. (2006) Detecting climate change induced range shifts: Where and how should we be looking? *Austral Ecology* 31(1): 22–29.

Soulé, M.E. (1991) Theory and strategy. In W.E. Hudson (ed.), *Landscape linkages and biodiversity*. Washington, D.C.: Island Press for Defenders of Wildlife, pp. 91–104.

Still, C.J., Foster, P.N. and Schneider, S.H. (1999) Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398(6728): 608–610.

Stone, P.B. (1992). *The State of the world's mountains: A global report*. London: Zed Books for Mountain Agenda.

Svenning, J.C. and Sandel, B. (2013) Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany* 100: 1266–1286.

Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.I. and Townsend, P. (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. *PNAS* 99(20): 12923–12926.

Thomas, C.D. (2011) Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology & Evolution* 26(5): 216–221.

Trofimov, V. (2008) Ecological geology, environmental geology, geoecology: Contents and relations. *Moscow University Geology Bulletin* 63(2): 59–69.

Troll, C. and Laver, W. (eds) (1978) *Geoecological relations between the southern temperate zone and tropical mountains*. Wiesbaden: Franz Steiner Verlag.

Tschakert, P. and Dietrich, K.A. (2010) Anticipatory learning for climate change adaptation and resilience. *Ecology and Society* 15(2).

United Nations (1993) *Agenda 21: Programme of action for sustainable development*. New York: United Nations Department of Public Information.

Van Der Windt, H.J. and Swart, J.A.A. (2008) Ecological corridors, connecting science and politics: The case of the Green River in the Netherlands. *Journal of Applied Ecology* 45(1): 124–132.

Venesky, M.D., Raffel, T.R., McMahon, T.A. and Rohr, J.R. (2013) Confronting inconsistencies in the amphibian-chytridiomycosis system: Implications for disease management. *Biological Reviews*.

Weldon, A.J. (2006) How corridors reduce indigo bunting nest success. *Conservation Biology* 20(4): 1300–1305.

Wellock, T.R. (2007) *Preserving the nation: The conservation and environmental movements, 1870–2000*. Wheeling, IL: Harlan Davidson.

Worboys, G.L., Francis, W.L. and Lockwood, M. (eds) (2010) *Connectivity conservation management: A global guide*. London: Earthscan.