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Connectivity conservation: maintaining connections for nature

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For the first time in Earth's long history, one species – *Homo sapiens* – completely dominates the globe. Over 6 billion people now inhabit the planet, and that number is growing at an alarming rate. In sharp contrast to previous eras, we drive, fly, telephone, and e-communicate from even the most remote regions of Earth. With the aid of technology, no significant segment of our population is truly isolated. Today, it is possible to make a cell phone call from the Serengeti, or live "off the grid" from in-holdings within the midst of national forests or wilderness areas in North America. With the notable exception of weedy species that thrive amidst the disturbances we create, predictably, the more "connected" we become, non-human life with which we share this planet becomes increasingly disconnected.

The vast reach of humans and the resulting parcelization of natural landscapes are of major concern to conservation scientists. Indeed, horror stories about habitat fragmentation appear in every book about conservation biology, make appearances in high-school textbooks, and are featured regularly in our leading newspapers and magazines. And conservation biologists are not alone in their concern about massive habitat destruction and fragmentation. Members of the public also have been inspired to promote special efforts for connecting landscapes in our increasingly dissected world.

While the vision of connected landscapes may be compelling, the practice of preventing fragmentation and conserving connectivity is not a simple matter. Conservationists often fail to articulate clearly what they

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mean by connectivity and what will be gained through their efforts to protect it, and often are insensitive to the logistical and economic costs associated with conserving landscape connections. Many questions remain unanswered. How essential is connectivity for biodiversity conservation? Do corridors – a primary tool employed to enhance connectivity – actually function as intended? Under what situations have human actions created too much connectivity, and how can we prevent it? Might there be better uses of conservation funds than attending to linkages that may or may not work? Such debates have raged within academic circles, not surprisingly spilling over to the rest of the conservation community as well. Nevertheless, the one point that remains clear is that the concern for connecting landscapes is increasingly becoming a part of land management worldwide. Despite its importance, however, the concept of connectivity is currently a loose amalgamation of related topics with little synthesis between them. The need to elucidate this concept therefore is more timely than ever.

In this introductory chapter, we explore the concept of connectivity and review the recent history of connectivity research in the scientific literature. Then, we briefly overview the benefits and challenges inherent in research and implementation of connectivity. Finally, we introduce the organization and content of the volume, and examine how linkages among the theoretical, empirical, and applied efforts discussed in this volume are essential for effective connectivity conservation.

WHAT IS CONNECTIVITY?

Within both the scientific and conservation community, confusion has existed as to what exactly connectivity is, how to define it, and how to measure successes of conservation programs attempting to protect it. At its most fundamental level, connectivity is inherently about the degree of movement of organisms or processes – the more movement, the more connectivity. Perhaps even more critical for those committed to biodiversity conservation is the converse – less movement, less connectivity. Movement in nature can take many forms: soil, fire, wind, and water move; plants and animals move; ecological interactions, ecosystem processes, and natural disturbances move, or elements move through them. All require, to different degrees and at different scales, connectivity in nature.

The idea of connectivity, then, is actually rather straightforward. What is not straightforward is the process of translating and quantifying the concept for scientific analysis and practical application. Connectivity is an entirely scale and target dependent phenomenon – definitions, metrics, functionality, conservation applications, and measures of success depend on the taxa or processes of interest and the spatial and temporal scales at which they occur. This fact is at the heart of differing perceptions and numerous academic debates regarding connectivity. As a result, one single, all-encompassing definition of connectivity has proven elusive, and authors throughout this volume tackle the concept of connectivity from a variety of perspectives, from metapopulations (Moilanen and Hanski Chapter 3) to landscape ecology (Taylor *et al*. Chapter 2), from the flow of energy, material, organisms, or information across dissimilar habitats (Talley *et al*. Chapter 5) to the flow of genetic material within and among populations (Frankham Chapter 4). As emphasized by Fagan and Calabrese (Chapter 12), clear, replicable, and pragmatic metrics of connectivity are vital if conservationists are to invest limited time and resources wisely.

Broadly, we can identify two primary components of connectivity (Bennett 1999; Tischendorf and Fahrig 2000; Taylor *et al*. Chapter 2): (1) the structural (or physical) component: the spatial arrangement of different types of habitat or other elements in the landscape, and (2) the functional (or behavioral) component: the behavioral response of individuals, species, or ecological processes to the physical structure of the landscape. Structural connectivity is often equated with the spatial contagion of habitat, and is measured by analyzing landscape structure without any requisite reference to the movement of organisms or processes across the landscape. Functional connectivity, however, requires not only spatial information about habitats or landscape elements, but also at least some insight on movement of organisms or processes through the landscape. Fagan and Calabrese (Chapter 12) further distinguish functional connectivity into two types based on the extent of available movement data: (1) potential connectivity: metrics that incorporate some basic, indirect knowledge about an organism's dispersal ability, and (2) actual connectivity: metrics that quantify the actual movement of individuals through a landscape and thus provide a direct connectivity estimate. As highlighted by Taylor *et al.* (Chapter 2), although structural connectivity may be easier to measure than functional connectivity, this does not mean that connectivity is a generalized feature of a landscape. That is, structural connectivity does not imply that the same landscape would have the same connectivity for multiple species or processes. Instead, a structurally connected landscape may be functionally connected for some species and not for others.

The discipline of landscape ecology, the study of the effects of landscapes on ecological processes (Turner 1989; Turner *et al.* 2001), has been instrumental in shaping our ideas about connectivity. Drawing from principles of landscape ecology, one of the first ecological papers to explicitly define connectivity was Merriam (1984), who introduced the concept of "landscape connectivity" and defined it as "the degree to which absolute isolation is prevented by landscape elements which allow organisms to move among patches." Taylor *et al.* (1993) later modified this definition to "the degree to which the landscape impedes or facilitates movement among resource patches"; this has since become one of the most frequently used definitions of connectivity in the scientific literature. Likewise, With *et al.* (1997) defined landscape connectivity as "the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure." Thus, by explicitly describing movement across landscapes, these definitions combine the structural and functional components of connectivity. In this volume, Taylor *et al.* (Chapter 2) return to the basics of landscape connectivity, revisiting these definitions, refining the concept, and providing advice for future applications.

Like landscape ecology, metapopulation ecology also has contributed much to our understanding of connectivity (Moilanen and Hanski 2001; Moilanen and Hanski Chapter 3). Some species naturally exist in metapopulations – a set of local populations within some larger area, linked together by occasional immigration (Hanski and Gilpin 1997; Hanski 1999). Because metapopulation persistence depends on sufficient colonization to compensate for local extinction of subpopulations, the concept of connectivity is a key feature of metapopulations. In this context, connectivity is generally related to migration rate, colonization rate, or gene flow among discrete patches in a metapopulation. Connectivity therefore is focused at the patch level, and is often measured as the distance to the nearest patch or nearest occupied patch. To distinguish this patch scale from the landscape scale discussed above, Tischendorf and Fahrig (2001) have proposed to label connectivity among patches, as used in metapopulation ecology, as "patch connectivity," and connectivity of the entire landscape, as used in landscape ecology, as "landscape connectivity." As described by both Taylor *et al.* (Chapter 2) and Moilanen and Hanski (Chapter 3), recent work is attempting to better integrate these various approaches to connectivity.

Notwithstanding the definitional nuances, the crucial point here is that the concept of connectivity, as viewed in the scientific literature, in conservation circles, in the media, and by the general public, is entirely dependent on the scale, species, or process in question. A landscape facilitating movement for an elephant may not do the same for a mouse – and vice versa. Connectivity also is by no means a static concept; rather, it is highly dynamic and often unpredictable; examples of the dynamic nature of connectivity are provided throughout this volume (e.g., Taylor *et al*. Chapter 2; Talley *et al*. Chapter 5; Harrison and Bjorndal Chapter 9; Ricketts *et al*. Chapter 11; Soulé *et al*. Chapter 25). Connectivity that is here today may be gone tomorrow – and vice versa. Lose sight of these facts, and confusion, and perhaps controversy, results.

RECENT HISTORY OF CONNECTIVITY RESEARCH

What are the historic trends of scientific research on connectivity? To explore this, we conducted a literature review (*Biological Abstracts*, February 21, 2005) to search for the keyword "connectivity" in scientific papers published from 1980 to 2004 in 23 major journals in conservation biology, ecology, landscape ecology, wildlife biology, and general science. Because corridors have tended to be a primary, and at times controversial, conservation tool to promote connectivity, we repeated this literature review searching for the term "corridor(s)." To correct for publication volume, we standardized the number of connectivity or corridor papers published each year by the total number of articles published annually in the 23 journals. Although limiting the search to keywords certainly underestimates the number of studies that actually investigated connectivity or corridor topics (see Moilanen and Hanski 2001), the results do provide some insight on patterns in connectivity research over the past two decades.

As evident by Fig. 1.1, research focused explicitly on connectivity is a relatively recent trend, one that mirrors our heightened concern of the impacts of accelerating habitat fragmentation. Out of about 67 500 papers published in these 23 journals during this time period, 328 and 352 papers had "connectivity" and "corridor" keywords, respectively. Corridor studies were relatively rare in the 1980s, but increased in prominence during the 1990s; this trend parallels the controversy within the scientific literature regarding the pros and cons of corridors as conservation tools (see below).

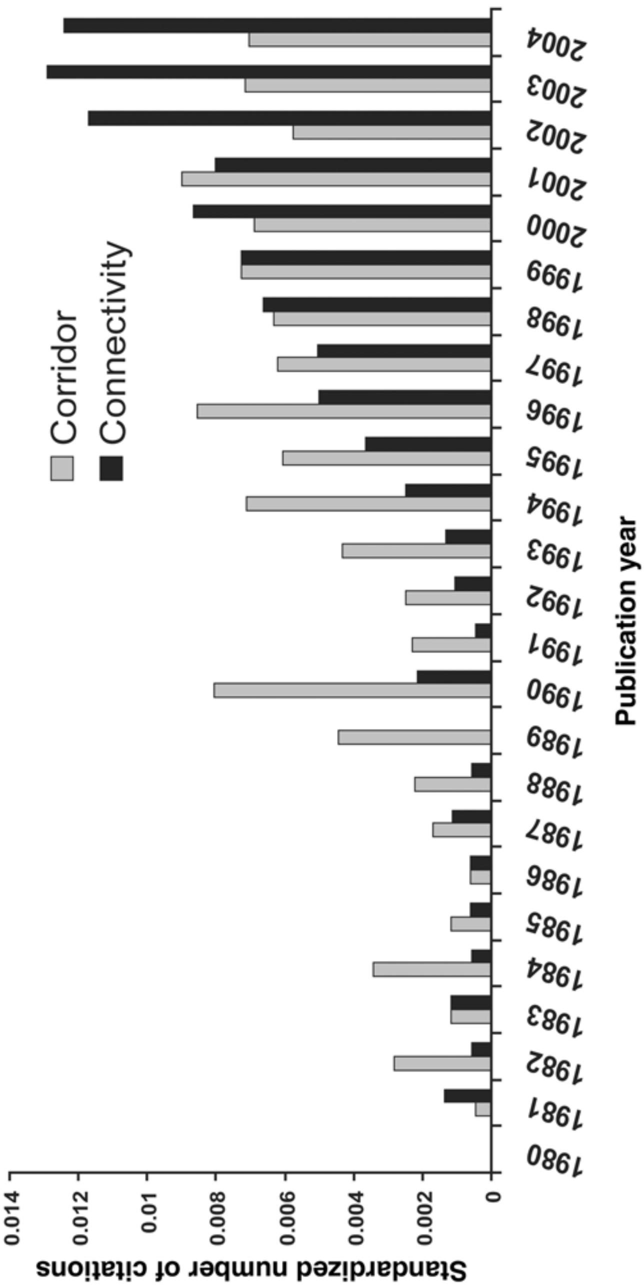

Fig. 1.1. Scientific papers published each year from 1980 to 2004 in 23 major landscape ecology, conservation biology, wildlife biology, and ecology journals with the terms "connectivity" or "corridor(s)" in their titles or keywords. The annual numbers of connectivity or corridor citations are standardized by the total number of citations in the 23 journals each year.

Studies focusing on connectivity have rapidly increased throughout the 1990s, and today outnumber corridor studies nearly two to one. Similarly, in a literature review of major freshwater ecology and management journals, Pringle (Chapter 10) found that freshwater connectivity studies, although a more recent trend than in landscape ecology and conservation biology journals, have proliferated within the last decade.

When analyzing connectivity and corridor studies by specific journal (Fig. 1.2), *Landscape Ecology* devoted more of its content to connectivity issues than any other journal; this result is intuitive given the history of connectivity research in the discipline of landscape ecology. Connectivity and corridor studies were next most frequent in conservation biology journals, again expected considering the conservation implications of connectivity research.

Although connectivity studies are on the rise, there is still much work to be done. For example, of the growing number of studies that have focused on movement through corridors, most have been descriptive and not experimental, thus limiting inference about the efficacy of corridors as conservation tools (Beier and Noss 1998; see below). Further, in an extensive review of the literature, Haddad and Tewksbury (Chapter 16) conclude that studies of corridor effects on population viability, community structure, and biological diversity are but in their infancy.

THE IMPORTANCE OF CONNECTIVITY CONSERVATION

Habitat fragmentation and the need for connectivity

How vital is connectivity for biodiversity conservation? We know that habitat destruction and fragmentation are the primary proximal threats to biodiversity (Wilcove *et al.* 1998). Fragmentation not only reduces the total amount of habitat available, but also simultaneously isolates the habitat that remains, preventing movement of organisms and processes in previously connected landscapes. Without natural levels of connectivity, native biodiversity is in jeopardy. Many studies have documented species loss in isolated habitats; even the largest protected areas existing today in western North America (Newmark 1987), eastern North American (Gurd *et al.* 2001), and even East Africa (Newmark 1995), are too small or too isolated to maintain viable populations for many wide-ranging species. As evident in this volume, while the effects of isolation are often most immediately noticeable for larger animals such as wide-ranging terrestrial carnivores (Paquet *et al.* Chapter 6; Tracey Chapter 14; Carroll Chapter 15; Theobald Chapter 17; Clevenger and Wierzchowski Chapter 20) and

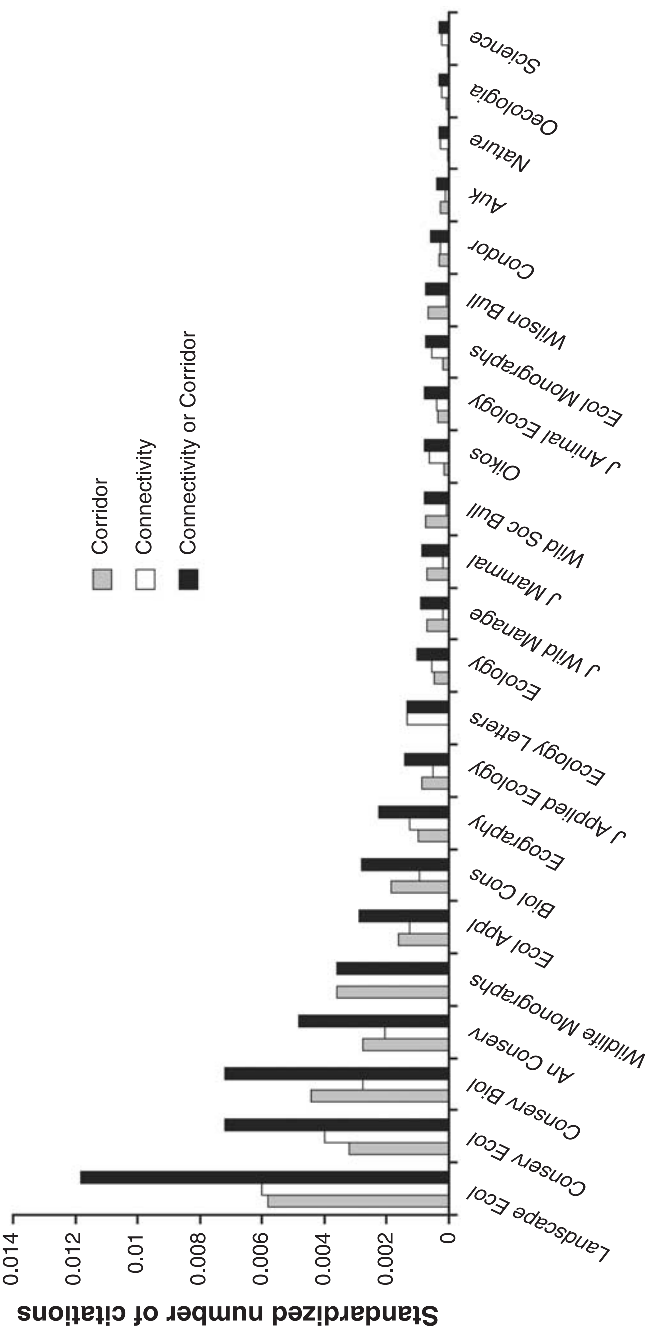

Fig. 1.2. Scientific papers published during the period 1980–2004 with the terms "connectivity" or "corridor(s)" in their titles or keywords, listed by each of 23 major journals in landscape ecology, conservation biology, wildlife biology, and ecology. The total number of connectivity or corridor citations are standardized by the total number of citations in the 23 journals.

migratory oceanic species (Harrison and Bjorndal Chapter 9), smaller animals such as freshwater shrimp (Pringle Chapter 10), marine invertebrates (Dibacco *et al.* Chapter 8), insect crop pollinators (Ricketts *et al.* Chapter 11), birds (Marra *et al.* Chapter 7), small mammals (Frankham Chapter 4), fish (Neville *et al.* Chapter 13), and butterflies (Moilanen and Hanski Chapter 3; Frankham Chapter 4; Haddad and Tewksbury Chapter 16) can all suffer when natural levels of connectivity are severed.

There are many, often synergistic, mechanisms by which isolation can lead to the extirpation of populations and the extinction of species. Demographic, environmental, and genetic forces, whether random or deterministic, can act independently or in concert to create a "vortex" of extinction in fragmented, isolated populations (Gilpin and Soulé 1986). Extinction vortices may be best repelled by preventing fragmentation and isolation in the first place, ideally by maintaining large populations in large contiguous blocks of quality habitat. Often, however, we must also attempt to maintain connectivity by protecting or restoring linkages in areas where fragmentation has already occurred. Indeed, although connectivity between reserves should certainly not be considered a substitute for the conservation of large core areas (Taylor *et al.* Chapter 2; Noss and Daly Chapter 23; Bennett *et al.* Chapter 26), connecting protected areas with linkages might be an effective way, and at times the last remaining option, to increase the effective area of some reserves and the population size of species in crisis.

Benefits and challenges of connectivity conservation

The preservation of natural levels of connectivity undoubtedly lends strength to efforts to protect species and habitats (Noss 1987, 1992; Hudson 1991; Saunders and Hobbs 1991; Noss *et al.* 1996; Noss and Soulé 1998; Bennett 1999; Soulé and Terborgh 1999; this volume). Possible benefits are many (Table 1.1). For example, connectivity may be essential to allow for the natural ranging behavior of animals among foraging or breeding sites and for the dispersal of organisms from their natal ranges (e.g., Tracey Chapter 14). Such movements may be critical to facilitate the exchange of genetic material among otherwise isolated populations (Frankham Chapter 4; Neville *et al.* Chapter 13); in the short term, genetic variability may be essential to mitigate the potential deleterious effects of inbreeding depression, and in the long term, to allow species to adapt and evolve to changing environmental conditions. Further, at large spatial and temporal scales, maintaining natural levels of connectivity may be essential to allow for natural range shifts in response to long-term

Table 1.1. *Potential advantages and disadvantages of the use of corridors as conservation tools to facilitate connectivity.*

Potential advantages	Potential disadvantages
(1) Increase immigration rate to a reserve, which could: (a) Increase or maintain species diversity (b) Provide a "rescue effect" to small, isolated populations by augmenting population sizes and decreasing extinction probabilities (c) Permit recolonization of extinct local populations, potentially enhancing persistence of metapopulations (d) Prevent inbreeding depression and maintain genetic variation within populations	(1) Increase immigration rate to a reserve, which could: (a) Facilitate the spread of infectious diseases (b) Facilitate the spread of exotic predators and competitors (c) Facilitate the spread of weedy or pest species (d) Decrease the level of genetic variation among subpopulations (e) Cause "outbreeding depression" by disrupting local adaptations and coadapted gene complexes
(2) Permit daily or seasonal movements for foraging, breeding, migration, or other behaviors	(2) Facilitate spread of wildfires and other catastrophic abiotic disturbances
(3) Facilitate dispersal of animals from natal ranges to adult breeding ranges	(3) Create a "mortality sink" by increasing exposure of animals in corridors to humans, native and exotic predators and competitors, pollution, and other deleterious "edge effects"
(4) Accommodate natural range shifts due to global climate change	(4) Riparian strips, often recommended as corridors, might not enhance dispersal or survival of upland species
(5) Provide predator-escape cover for movement between patches	(5) High economic cost to purchase, design, construct, restore, maintain, and protect corridors
(6) Provide wildlife habitat for transient or resident animals within corridors	(6) Trade-off costs and conflicts with other conservation acquisitions, including conventional strategies for enlarging core areas and preserving endangered species habitat
(7) Provide alternative refuges from large disturbances (a "fire escape")	(7) Political costs from altering human land-use patterns
(8) Continuance of ecological processes and ecosystem services such as succession, seed dispersal, and flow of water, nutrients, and energy	
(9) Provide "greenbelts" to limit urban sprawl, abate pollution, provide recreational opportunities, and enhance scenery and land values	

Source: Modified from Noss (1987); see also Soulé and Simberloff (1986), Simberloff and Cox (1987), Soulé (1991), Hobbs (1992), Simberloff *et al.* (1992), McEuen (1993), Rosenberg *et al.* (1997), Beier and Noss (1998), Bennett (1999), Dobson *et al.* (1999).